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PHYTOGEOGRAPHY OF THE EASTERN MOUNTAIN-FRONT IN COLORADO

I. PHYSICAL GEOGRAPHY AND DISTRIBUTION OF VEGETATION

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 251

ARTHUR G. VESTAL

(WITH SEVENTEEN FIGURES)

Introduction

The plant geography of a region is the effect of the working of present and former environmental influences upon the floras and vegetation-complexes which exist and have existed within the region and in the regions adjoining. The region of present study, lying as it does in the transition belt between two great geographic divisions of North America, the Great Plains, or western part of the prairie region, and the Rocky Mountains, has some of the characters of both; others of its physical and vegetational features are transitional, intermediate; and it has certain peculiarities, differing thus from the regions on either side. Since climatic variation, differences of soil and of topography, and multiformity of vegetation-types are considerable, the plant-covering of the area is a complex of many diverse types. Descriptive accounts of the plant associations of plains and foothills have already been published (**17**, **18**), so that the present article may deal more particularly with geographic description and geographic relations.

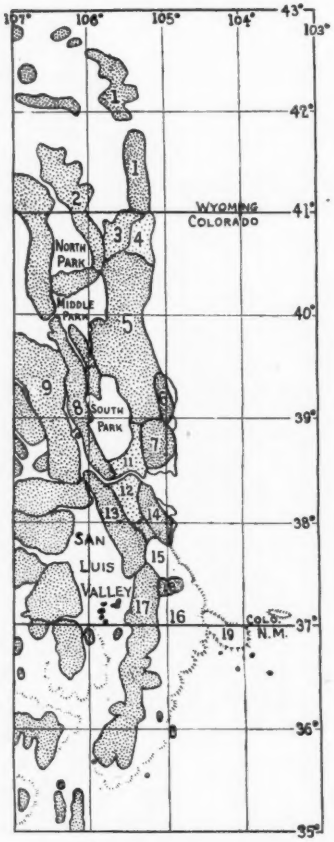


FIG. 1.—Map of southern Rocky Mountains, except westernmost ranges; mountain areas shaded; names of areas indicated by numbers are: 1, Laramie Mountains; 2, Medicine Bow Range; 3, low mountain area connecting Laramie and Front ranges; 4, foothills of Poudre River area; 5, Front Range; 6, Rampart Range; 7, Pike's Peak highland; 8, Park Range; 9, Saguache Range; 10, Upper Arkansas Valley (between 9 and 8); 11, low mountains; 12, Wet Mountain Valley; 13, Sangre de Cristo Range; 14, Wet and Greenhorn mountains; 15, Huerfano Park; 16, southern sedimentary plateau; 17, Culebra Range; 18, Spanish Peaks highland; 19, Raton mesas.

While in general the plains and mountains contrast rather sharply at their junction, this is not always true; the mountain-front is a transition zone in places a number of miles broad rather than a line. It is not determined alone by altitude, by topography, by character of the bedrock, or by climate; it is the resultant of all of these. For the sake of clearness the foothills may be described as the drier and less elevated (about 5800–8000 ft.) part of the mountain plateau, with vegetation composed of grassland, scattered rock pines, and a few other trees (*foothill zone*, RAMALEY 8). Except in the southern "sedimentary plateau" (fig. 1), perhaps rather to be considered part of the mountain-front area, the foothills may be said to comprise the granitic hills of the mountain-mass proper; while to the mountain-front zone may be assigned the upturned sedimentary hogbacks and longitudinal valleys, sedimentary outcrops, buttes and broken plateaus, and the mesas and upper parts of the débris-covered slope to the plains. The vegetation is of the greatest variety. The plains proper may be said to commence where the mixed soil and

vegetation of the detrital outwash from the hills is succeeded by the fine soil and mostly short-grass vegetation of the shale beds covering most of the Great Plains surface.

Plan of presentation.—The writer has been much influenced by the work of DAVIS (1) on the geography of the Colorado Front Range, a regional presentation and particularly relevant in this study, since the area considered is so nearly the same. DAVIS' systematic treatment avoids repeating descriptions of frequently encountered land-forms by recognizing their common features and giving each a brief characterization and a name, thus identifying them when mentioned later. Minor differences of detail are not considered in the condensed treatment thereby made possible. In a regional study, in which numerous elements form an intricate complex, this omission of detail is essential. As the physical geographer refers land-forms to types (mental counterparts of physical realities), so in a regional study of plant geography one may refer forms of vegetation to types which are the same over considerable areas. This is a common practice in ecological classification, but many studies of limited areas of vegetation have characterized the plant communities without regard to geographic orientation. If possible, local representations or variants of widespread associations should be recognized as such. The characterization of the relatively few widespread and important vegetation-types makes it possible to systematize plant geography. This systematic treatment emphasizes the common features, the resemblances of similar plant communities, but the differences, when worthy of note, can always be stated in addition. The section of this study which is here published is the systematic part, which establishes the types of topography, soil, climate, and vegetation as developed in the region or in parts of it. It will be followed by a regional section, which describes the physical and vegetational features "in their actual spatial relations," to use the words of DAVIS, and by parts dealing with general geographic and developmental relations of the vegetation.

Physical features

The area studied is the eastern front of the Rocky Mountains in Colorado, of which the most characteristic part is the Front

Range. This has been studied by many geographers, more recently by DAVIS. The Front Range has been described by him as a submaturely dissected upland of crystalline rocks, elevated above the plains to the east by a long north-south monoclinal fold. The tops of most of the hills form the remains of a peneplaned surface, the result of the erosion following the uplift, with complete removal of the sedimentary layers from the raised area on the west. A few

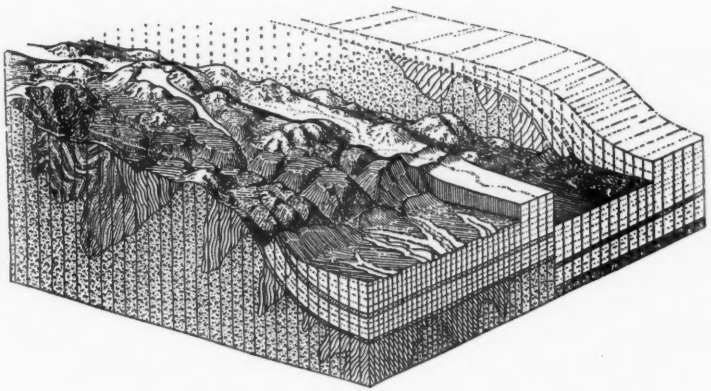


FIG. 2.—DAVIS' block diagram of Front Range (reproduced with author's permission from 1): at right is condition following first uplift with monoclinal fold; next part shows peneplaned upland with monadnocks and cuestas (hogbacks); third shows entire region after second uplift; last block on left shows present condition, with glacier-carved range-crest, gently sloping, dissected, crystalline upland, of which lower and eastern part forms foothills, and mountain-front, with sloping crags, cuestas, and longitudinal valleys; outside may be seen débris-covered terraces and broad valleys of streams running out into plains.

monadnocks surmount the general level. The present eastward inclination of the old peneplain and its dissected character in the crystalline area, and the removal of sedimentary strata of the plains to a depth far below the foothills, are the effects of a second uplift, an uparching of the whole region, and of the subsequent cycle of erosion. Near the base of the original fold the sedimentary strata are sharply upturned against the outer granitic slopes, the ends of the resistant strata forming ridges and sloping crags (fig. 2).

The outer slope to the plains has been described by JOHNSON (5) as a débris-apron or composite of alluvial fans, of which the profile is that of a stream-grade, rapidly flattening into the very slight and uniform incline of the Great Plains. The graded surface is covered by unassorted rock-waste from the hills, which thins out and becomes finer in texture toward the east; it is absent from most of the surface of the plains, which is of fine grained residual soil. This grade is that of the High Plains;[1] the streams have very generally cut below it, especially near the mountains. The Platte and Arkansas rivers, the trunk-streams, have cut very broad valleys in the soft shales of the plains. The north-south valleys of their tributaries which parallel the mountain-front are bordered on the east by escarpments of considerable height and are notable geographic features. This recent downcutting, where working in soft shales just outside the foothills, leaves many terraces, remnants of the older and higher stream-grade levels; their covering of rock-waste preserves their flat tops. They are generally known as "mesas"; although not true mesas, the term is convenient.[2] Where the upper sedimentary beds consist of sandstone or limestone, extensive plateau areas with deep canyons, buttes which may be numerous or scattered, or simple escarpments may be encountered. In a few places igneous intrusions are seen as dikes or as basaltic layers capping large mesas (true mesas in this case). From these features the mountain-front zone derives its varied character; the mountain upland on the west, and the plains extending far to the east, are of less irregular structure.

Arrangement of the component ranges and smaller ridges *en echelon* is a notable feature of the easternmost line of mountains. Ranges which are in general north and south of each other are themselves oriented with the northern end a little to the west. MARVINE writes (7, p. 132):

[1] The distribution of the remnants of the High Plains may be seen in a map by JOHNSON in the article mentioned.

[2] A true mesa is a tableland capped by a more resistant stratum which keeps the top flat by retarding erosion except on the sides. The débris-covered terraces flanking the mountains are like a true mesa in that the rock-waste layer acts as a more resistant cap.

In traveling from the north along the zone of hogbacks lying at the base of the mountains southward, the traveler finds the mountain-slope directly west of him falling lower and lower until it becomes an insignificant ridge, and finally dies away in the plains.

Passing around the southern end of the diminishing ridge the main mountain-slope is found lying several miles to the west, and separated from the ridge by a baylike valley extending northward behind it. . . . . The ridges are uplifted or anticlinal folds, the valleys depressed or synclinal folds, both dying away southward into the flatness of the plains.

The minor embayments due to echelon arrangement may be made out only in a large scale map, but the major embayments at the south end of the Rampart Range, the Pike's Peak highland, and the Greenhorn Mountains can easily be seen in fig. 1.

A more detailed view of the typical land-forms and vegetation-forms encountered in passing from mountains to plains traverses the several north-south zones in the following order: first the granitic foothills; then the transition zone of the mountain-front, with its upturned ridges, its mesas and graded slopes, and in places its plateau areas, buttes, and escarpments; and lastly the plains themselves.

GRANITIC FOOTHILLS

The mountain plateau is in most places submaturely dissected, the original upland level being represented only by the rounded tops of the hills (fig. 3). Slopes and summits are thinly covered with rock-waste. Occasional resistant dikes and ledges give craggy exposures of massive rock, not covered by any soil or débris. Below these, or on the sides of steeper ravines, are talus slopes of variously sized rocks, or slides of "granite-gravel."[3] Table I is a synopsis of topographic areas of the foothills arranged as habitats, and, correlated with these, the characteristic vegetation-types. Edaphic conditions largely determined by topography (local position in relation to surroundings, direction, amount of slope, and soil texture) have been discussed in the account of foothills vegetation (**18**).

This two-column form of presentation is adopted as being concise, as emphasizing relations between physiographic and ontographic features (the environment and the environed), and as permitting a more comprehensive view of the whole complex and its

[3] Decomposed granite in small angular fragments.

parts than can be obtained by the linear arrangement. Geographers will note that topographic *areas* rather than *land-forms* are used as the units of area of physical conditions (habitats), since land-forms, such as mesas and ravines, may include several topographic areas presenting quite diverse environmental conditions. Moreover, a single topographic area, even if physically uniform, may allow the growth within it of several more or less distinct vegetation-types.

FIG. 3.—Maturely dissected foothills near Boulder Creek: pine-sprinkled, rather than forested, surface mostly covered with dry grassland.

A brief statement concerning mountain parks may be made. These are small plains or flat valleys shut in on all sides by hills. They are not well developed in the foothills as compared with the montane zone. They are mostly formed where one of the principal eastward flowing streams is joined by tributaries from valleys opening into the park. There is a single outlet. Many of the montane parks in the Front Range contain the terminal moraines of former valley glaciers from above, and their topography is in large measure the work of ice. The slight gradient causes many

TABLE I

TOPOGRAPHIC AREAS (HABITATS) AND ASSOCIATED VEGETATION-TYPES IN GRANITIC FOOTHILLS COMPLEX

TOPOGRAPHIC AREAS	VEGETATION-TYPES
The geographic mean is that presented by rather exposed and xerophytic sloping surfaces, thinly covered with rock-waste of mixed texture, rather gravelly and with surface rocks. Local departures from the general condition are as follows:	The general ground-cover is mixed foothills grassland and primitive grassland, largely of grasses and herbs of the plains, with admixture of Rocky Mountain herbs, not all xerophytic. Scattered rock pines and plants of the mixed shrub association, singly or in clumps, dot the surface. In special habitats occur:
1. Exposed rock surfaces (bowlders and rock-walls)	1. Xerophytic lichen association
2. Rock-crevices	2. *Selaginella*, shrubs of *Jamesia* and *Ribes*, rock pine
3. Rock-strewn detritus slopes	3. Mixed grassland, and mixed consocies of primitive grassland, with higher proportion of woody plants (rock pines, mixed shrub, *Ceanothus*, *Arctostaphylos*)
4. Rock-talus	4. *Artemisia frigida-Koeleria* consocies of primitive grassland (18)
5. Compacted granite-gravel floors and side-slopes	5. Compacted granite-gravel consocies of primitive grassland (18) with rosette plants; *Arctostaphylos*
6. Loose granite-gravel floors, washes, and talus (gravel-slides)	6. Primitive grassland, with *Geranium-Chrysopsis* consocies, mat (rosette) consocies of gravel-slides, etc.
7. Mixed-soil floors and detritus-slopes (fine soil with imbedded and superficial rock-fragments of various sizes)	7. Foothills mixed grassland, with addition of other components, *Ceanothus*, sumac, pine, etc.
8. Fine-soil floors and detritus-slopes (infrequent)	8. Foothills mixed grassland, of a form approaching plains short-grass
9. Less xerophytic side-slopes (mostly north-facing, mostly of considerable gradient, and best developed in valleys)	9. Mixture of mixed shrub, rather less xerophytic mixed grassland, and pine associations, with representatives of canyon forest and scattered trees of *Pseudotsuga*
10. Narrow mesophytic ravines (best developed as small side-canyons, especially on the south side of eastward flowing main streams)	10. Mesophytic representations of mixed shrub, *Pseudotsuga*, aspen, *Symphoricarpos*, canyon forest, and mesophytic grassland associations. Mosses, *Saxifraga*, etc., in wet rock-crevices
11. Stream-sides in shaded ravines	11. *Betula*, *Alnus*, *Corylus*, and *Acer glabrum* of the canyon forest; shrubs; moist-soil herbs, as *Heracleum*, *Rumex*, etc.
12. Stream-sides in open canyon bottoms	12. *Populus angustifolia*, willows, etc.

meanders and oxbows in the streams, and there are in some parks small lakes in morainal depressions. The stream-sides are frequently boggy, with meadows adjoining. The parks are mostly treeless, or nearly so, and show no signs of former or impending forestation. The exposed dry flats are covered with dry grassland, its composition depending on altitude and geographic position chiefly. Differences in soil texture cause local variation of the grassland, but this is less marked and less minutely local than on the hill slopes. Certain lower areas are occupied by meadow and sedge communities, and the rolling surfaces of moraines (in montane parks) are variable in soil texture, soil moisture, and in the composition of their grassland cover; but the greater part of park floors is well drained, flat, and quite uniformly covered with dry grassland. This vegetation, in any one park, forms what might be called a crystallization of the grassland of the neighboring hills, whether in foothills or montane zone, in view of the comparative uniformity of the grassland of the flats as contrasted with that of the diversified slopes of hill topography. The lower parks have a grassland cover very like that of coarse soil in the mountain-front area or in the plains (see description of Estes Park in the regional section). The higher parks have fewer plants of the plains and more of the mountains. There is a floristic and vegetational gradation from plains grassland through the lower parks to montane grassland as seen in the higher levels. The parks thus show a steplike series of floristic and ecological changes with altitude. RAMALEY (10, 11) for some years has studied park vegetation, especially in Boulder Park at Tolland, Colorado, on South Boulder Creek.

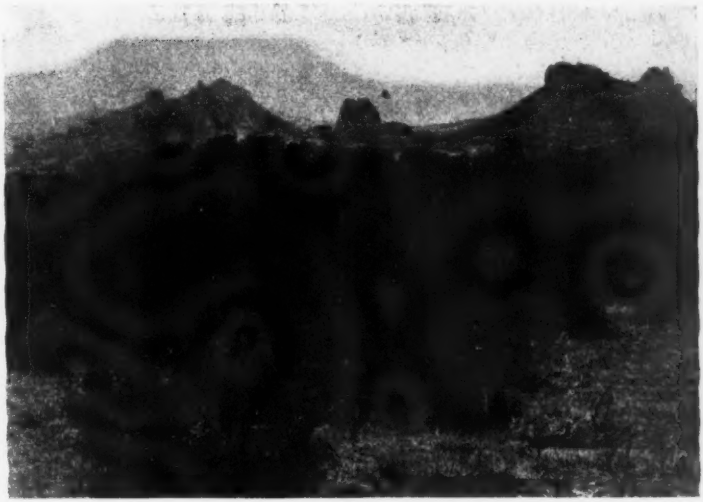
TRANSITION AREA OR MOUNTAIN-FRONT ZONE

The sedimentary rocks, lying upon the granite, are upturned at the monoclinal fold, and are seen in a horizontal series of exposures of strata, the lower and older members abutting on the granitic foothills to the west, the upper formations outcropping in order toward the east. Since the tilting at the mountain-front is for considerable distances greater than 45° (locally reaching 90° and even more, resulting in overturns), the lower formations have narrower zones of outcrop than the upper strata, which dip so slightly as to cover areas many miles wide in the plains. The

narrow zone of older and lower strata contains alternating resistant and soft members, giving rise to the hogback ridges and intervening valleys already mentioned, while the newer rocks are mostly soft shales and sandstones, giving a flat or rolling topography over the surface of the plains, with occasional escarpments at the edges of stream-valleys. Both angle of dip and hardness of rock, therefore, contribute to a differentiation, in the sedimentary area outside the foothills, of a relatively narrow ridge-valley mountain-front zone from the very broad and mostly flat plains region.

Just outside the ridge-and-valley zone is the graded slope to the plains, covered with rock-débris and dissected into terraces or mesas of varying level. In places along the mountain-front the ridge-and-valley topography is absent or poorly developed, either because the troughs are not yet carved beneath the slope from the granitic hills, or because the ridges are already planed (locally) to a graded floor. The terraces are also missing from certain parts of the mountain-front. The topographic complexes of the ridge country and of the mesa country may now be described separately.

THE HOGBACK RIDGES (CUESTAS) AND INTERVENING TROUGHS (figs. 4, 5).—Two of the numerous sedimentary strata overlying the crystalline rocks are so resistant as to form ridges over great lengths of the mountain-front. These two strata are of such conspicuous geographic importance that they merit distinctive names and since many persons know them by their geological names, these will be used here in a geographic capacity. The *Fountain* sandstone, which in most places lies directly upon the granites, is very thick, and is composed of dark red, rough arkose materials, variable in texture. It is in places more resistant than the granites, so that side-gulches tributary to the east-flowing streams of the foothills are common in the granite just beneath the Fountain. Continuous troughs between the Fountain and the granite are not frequent. In many places the hard red sandstones form broad smooth-faced crags lying upon the outer foothill slope, reaching maximum size in the well known "flat-irons" south of Boulder (fig. 6). The other hard stratum is the massive gray sandstone known as the *Dakota*. It is separated from the Fountain by several less resistant strata of considerable aggregate thickness,



FIGS. 4, 5.—Upturned sedimentary ridges of mountain-front zone: fig. 4, eastward view in Perry Park, where a broad flat valley has been leveled between ridges and outer granitic foothills; floor of flat is of compacted angular fragments; vegetation is primitive grassland alternating with scrub oak; Dawson Butte in far background; fig. 5, southward view, between Golden and Morrison, of longitudinal valley inside Dakota hogback, shown on left in long curve.

and is usually seen as a bold ridge parallel to the outer slope of the foothills some distance to the east. The term "hogback" is familiarly applied to the steep Dakota cuesta.

A deep and wide trough usually extends between the Fountain crags and the Dakota cuesta. The upper part of the east-facing slope of this trough is the outcrop of a "creamy sandstone," which in places forms prominent outcrops, or even strong ridges, as at Morrison at the mouth of Bear Creek. Just east of and below the creamy sandstone is an easily eroded shale, which gives its rich red color to the deep soil of the valley. The west-facing slope, below the Dakota crest, is the outcrop of a calcareous sandstone stratum which is weathered so slowly as to be covered only by a thin soil. In certain places this limy sandstone stratum is hard enough to form a separate ridge or hogback crest.

The Dakota hogback is one of the most constant and conspicuous topographic features of the mountain-front, since it is practically everywhere harder than the strata above and below. Its top is usually quite even and straight, representing the level of a former graded surface. Its crest is quite rocky; there is no soil except in the crevices.

The present graded slope to the plains begins usually with the outer slope of the Dakota hogback, through first a layer of dark shales, then a thin limestone overlaid by soft light-colored shales, then clays and shales. Near every east-flowing stream, however, the graded slope is likely to be cut beneath by side-gulches cutting down into the dark shales, leaving a cut-off mesa with the limestone at its high western end.

Local distribution of vegetation in the mountain-front belt of upturned sedimentary rocks presents a variability apparently dependent almost entirely upon topography and soil texture, just as in the area of granitic foothills. There seem to be few if any perceptible differences in the floras of the different geological formations which can be traced to chemical differences in the substratum. It is perhaps true that cedars are more frequent in the limestone or calcareous sands of the stratum just below the Dakota, where these are exposed in gulches which notch the Dakota hogbacks, and that there are certain slight floristic differences between

granitic and sedimentary areas. This question has been discussed by RAMALEY (9), who found the two areas about the same in floras (in the Poudre mountain-front area), with *Cercocarpus* abundantly represented in the sandstone but not in granite, *Selaginella* apparently absent from the sandstone, and lichens infrequent there. Following a suggestion from COWLES, it appears to the writer that differences in rate of erosion of the substratum may explain the distribution of lichens, and perhaps *Selaginella* also. The sandstones are rather soft in the Poudre area, and wear away too rapidly for the lichens to establish themselves abundantly. The Fountain sandstone is harder in the Boulder region than elsewhere, and there at least it bears lichens almost as abundantly as do the granites. *Selaginella* is frequent in the sedimentary rocks in the Boulder area, as RAMALEY has pointed out. The writer knows of no plants which are restricted to either sedimentary or granitic areas, the only observed differences being those of relative abundance. The gulches, exposed slopes and crests, etc., of the sedimentary area are quite comparable to similar topographic situations of the granitic foothills, and have practically the same plant assemblages.

The rocky upper slopes of the Fountain, the Dakota, and other ridge-making strata, where they occur, lack soil except in crevices, and are mostly bare, except where rock pines or pinyons, shrubs of rocky situations (*Cercocarpus*, *Ribes*, *Jamesia*, etc.), and crevice plants, including many xerophytic herbs, can obtain a foothold. The west slope of hogbacks is blufflike, usually, and rocky, while the east slope is less steep (depending on the local angle of dip) and likely to be strewn with débris, as are the slopes of the harder exposures of the valley, and these have shrubby or herbaceous vegetation, sparse, and of species of rocky situations. The softer shales occupying the bottom of the valley are usually deeply buried by débris (of fine soil with imbedded rock fragments of all sizes), and support a grassland vegetation, which is luxuriant in the rainier parts of the growing season and very dry the rest of the time. A stream-bed in the bottom of the valley may be bordered by a strip of mixed shrub, *Crataegus*, oak, or canyon forest; or if dry, by scattered narrow-leaf cottonwoods and willows. Mesophytic

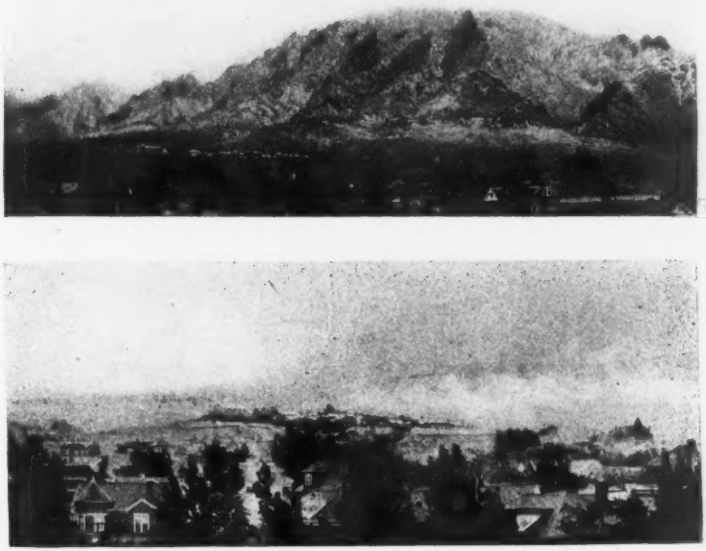
ravines developing in the sedimentary area support mixed-shrub, woodland, or mesophytic herbaceous growths, as in the granitic foothills. Local meadows (mesophytic grassland) are found on slopes where seepage or a high water table moistens a deep soil for at least part of the growing season.

In places the sedimentary rocks have been worn down more than is common, so that they are mostly or in part reduced to a general grade, above which the more resistant layers rise locally. This is the condition in the valleys of some of the larger streams from the foothills, and is seen at Platte Canyon, partially at Bear Creek (Morrison), and also in Perry Park (fig. 4) and the Garden of the Gods. The floor of this graded surface, especially in the Fountain exposures, is likely to be covered very thinly with small angular fragments, loose or compacted. The vegetation, as well as the soil, is very like that of gravelly floors in the foothills, being a variant of the primitive grassland association, with scattered rosette or mat plants, *Bouteloua hirsuta*, etc.

The climatic transition in the zone of upturned sedimentary strata is rapid. At Boulder and elsewhere dense cloud-banks have frequently been seen to descend to or just beneath the Fountain crags without continuing outward and downward to the plains (figs. 6, 7). The outer granitic hills and upper sedimentary slopes receive greater and more frequent precipitation than the lower slopes and adjacent mesas and plains; it may rain slightly below while it snows considerably above (cf. fig. 12); the outer and lower slopes are more exposed to wind, less cloudy, and in places less shaded from the afternoon sun by the higher granitic hills than the inner valleys and upper slopes. No exact data are available for this sudden climatic transition. Where the outcrop of sedimentary ridges and valleys is wide, as in the northern mountain-front region, the outer hogbacks are severely exposed to sun and wind, as in the open plains. Their coarse rocky soil favors woody plants; the xerophytic *Cercocarpus* shrub assemblage is here more extensively developed than anywhere else.

MESAS AND GRADED SLOPES OF THE DÉBRIS-APRON (fig. 8).—The general character of the graded slopes and their mesa-fragments has already been suggested. The mesas are of varying ages and

levels. They are described in the accounts of LEE (**6**), JOHNSON (**5**), FENNEMAN (**2**), SHANTZ (**15**), RAMALEY, ROBBINS, and DODDS (**12**), and VESTAL (**17**). The topographic parts of a mesa are: (1) the



FIGS. 6, 7.—Climatic transition at mountain-front: fig. 6, outer mountains just south of Boulder, seen from university campus; clouds beginning to form at summit of Green Mountain, while much of South Boulder Peak, at extreme left, is already obscured; snow covers the mountain slopes and fades out toward base of high mesas; roofs of distant buildings also white; fig. 7, practically same view, a little later, with upper slopes obscured; at one time it began to snow on mountains and upper mesas, and a few minutes later to rain in town; shortly afterward it changed to snow in the upper edge of town, so that the roof of the building with the short steeple at the right in midground, and of nearer houses, were well whitened, while rain still fell on the campus, less than half a mile away, and not more than 50 ft. lower; difference in elevation at mountain-front is critical as regards climatic change.

mesa-top, with flat surface covered with mixed rock-débris; (2) the edge or mesa-crest; (3) the side-slope; and (4) valleys or draws in the side-slope. The soil conditions and their effects on plant distribution have been discussed in the three articles last cited.

The débris-cover, where it has not been removed by recent erosion, extends far out into the plains. Its removal from the extensive areas of soft shales and clays marks a change from the flat terrace level to the easily eroded, gently rolling surface of much of the plains. The High Plains are extensive remnants of the old graded surface, away from the mountains.

The north-south distribution of the terraces is practically that of the mountain-front, although as conspicuous topographic forms the mesas are not so extensive. So far as effects on distribution of vegetation are concerned, the presence of the coarse mixed soil of

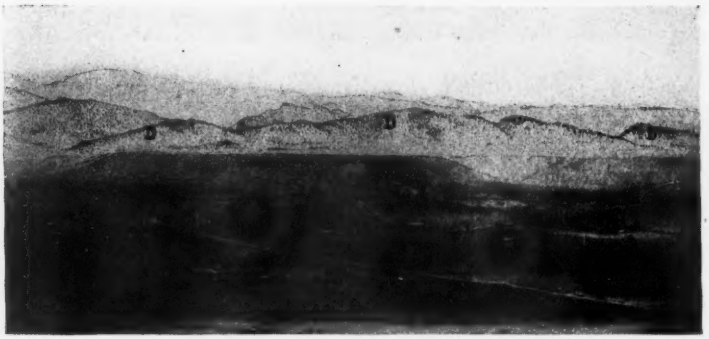


FIG. 8.—Table Mesa, about 7 miles north of Boulder; outlines of hills sketched in with ink; ridge DDD is Dakota hogback; Boulder mesas may be seen in figs. 6 and 7.

the detrital surfaces is the important physical condition. It permits the growth in the same small area of a rich variety of plants, representing numerous vegetation-types and different geographic elements.

PLATEAU AREAS, BUTTES, AND ESCARPMENTS (figs. 9–11).—Where the sedimentary strata are horizontal or of rather slight dip the harder layers protect the softer rocks beneath, and extensive plateau surfaces are left above the grade established by present erosion. These can be invaded only at the edge and by ravines which eat their way headward into the bluffs. Smaller elevated areas or buttes, recently or long ago cut away from plateaus by

meeting of two such ravines, are common. Older buttes are fewer and more distant from one another.

FIGS. 9, 10.—Buttes and plateau areas: fig. 9, North Table Mountain at Golden, west of Denver; this and South Table Mountain are capped with basalt; fig. 10, Fisher Peak, northern end of Raton mesas, as seen from valley of Purgatoire River, a few miles above Trinidad; upland in midground belongs to southern sedimentary plateau; vegetation is principally dry grassland with scattered pinyons and cedars and infrequent clumps of scrub oak.

The plateaus and buttes are found outside of the upturned ridge and valley zone wherever the surface rocks are rather resistant. These resistant strata are usually the most recent and uppermost,

although the much older Dakota is at the surface over considerable areas in the plains drained by the southern tributaries of the Arkansas. For a considerable thickness above the Dakota the strata are mostly soft shales, which erode too readily to give tableland topography.

The larger through streams and their tributaries have cut below the level of the High Plains, leaving escarpments which are particularly notable near the Platte-Arkansas divide. Plum and

FIG. 11.—Buttes and plateau areas: divide between East Plum and West Plum creeks, in Castle Rock area, showing some of rhyolite buttes; one of the most imposing of these, Dawson Butte, shown in fig. 4.

Cherry creeks, running north into the Platte from the divide, and Monument, running into Fountain Creek, south to the Arkansas, have eroded deep valleys parallel to the mountain-front. Away from the mountain-front proper these valleys are bounded by lines of steep cliffs, but the west border of Monument and West Plum Creek valleys is the graded slope from the foothills, with its débris-covered terraces. Isolated buttes are present within these valleys, some of them protected by caps of igneous rocks from local outflows.

The southern part of the Sangre de Cristo Range (sometimes considered as a separate mountain chain, the Culebra Range) is flanked on the east by a sedimentary plateau which rises abruptly above the plains in a steep line of bluffs. The plateau is of sandstones mostly, of slight dip, and is much dissected by the eastward

flowing streams and their tributaries. On it rests the highland of the Spanish Peaks, and it is ribbed by resistant dikes of igneous material from two outflows, one set radiating downward from the peaks themselves. With the plateaus should be classed the high lava-capped mesas of the mountain-front and plains in the area near the Colorado–New Mexico boundary.

As in the hogback ridges, vegetation distribution in the plateau and butte areas is largely determined by soil texture and topography. Atmospheric conditions vary with exposure to wind and sun. The tops of the plateaus are covered with short-grass and

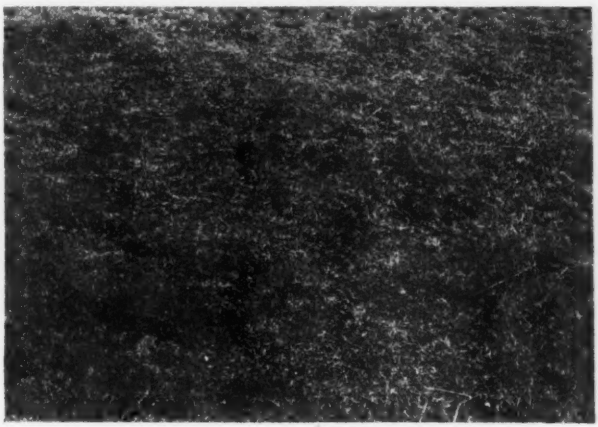


FIG. 12.—Unbroken short-grass ground cover in plains

mixed grassland over the level upland stretches of comparatively fine-textured soil. Exposed cliffs and crests, and rocky débris-slopes, afford lodging places for woody xerophytes (*Cercocarpus*, rock pines, pinyons, and cedars), with primitive grassland as the general ground-cover. The deeper and shaded parts of canyons and ravines approach a mesophytic condition, with mixed shrub and woodland vegetation.

PLAINS

Plains topography is typically flat or gently rolling country, with fine clay soil from a soft-shale substratum. Short-grass is the characteristic vegetation (fig. 12). Where the substratum is

sandstone, the soil is more porous, with much sand; and plants of an assemblage typical of sandy soil are seen (17). Sand hills are present locally, usually to the leeward of larger streams.

Near the mountains the débris-cover, if present, considerably modifies topography, soil conditions, and vegetation. It may extend a long way into the plains, or may have been removed very near the beginning of the graded slope from the foothills.

Saline or alkaline areas are locally present. The valleys of the Arkansas and its tributaries (wet-weather streams, many of them, with trenched flood-channels) are in many places alkaline, and show prominent stands of *Sarcobatus-Chrysothamnus* vegetation.

Woody vegetation from the foothills extends locally far into the plains in rock outcrops, and along stony crests of stream-bluffs or terraces. The larger streams are bordered for many miles from the mountains by cottonwoods, usually scattered.

Climate

The region has a continental climate, semi-arid, less so at the base of the mountains and in the foothills, with most of the rainfall in the warmer months. Wind movement, proportion of sunshine, and evaporating power of the air are high in the plains, with wide extremes of temperature; all of these features are less marked in the foothills.

The southern part of the region is warmer and drier than the northern, and with different distribution of rainfall. The rapid east-west change in elevation and topography at and near the mountain-front is accompanied by more or less considerable climatic variation; this with the local peculiarities occasioned by the elevated Platte-Arkansas divide, and the differences between areas north and south of the divide, may be seen in the summaries of climatic data for the particular subregions. These data have been taken from the summary of Climatological Data for eastern Colorado, southeastern Wyoming, and northeastern Colorado.[4] The facts shown in table II should be considered in the light of their

[4] Section 6, northeastern New Mexico, by C. E. LINNEY. Section 7, region drained by the Arkansas in Colorado, and section 8, region drained by the Platte in Colorado, by F. H. BRANDENBURG. Section 24, southeastern Wyoming, by W. S. PALMER.

determinative influence upon the vegetation; this can be done in only the barest manner in this section, but these relations are again brought out in the part on geographic relations of the vegetation.

Temperature conditions of the different parts of the region may be summarized as follows: The foothills have a lower mean temperature and shorter period without frost than either plains or mountain-front. Certain of the foothills vegetation-types and

TABLE II

TEMPERATURE DATA

Area	Average mean temperature ° F.	Maximum temperature	Minimum temperature	Average number of days in growing season
Foothills (4)	43.1	100	−36	99
Northern (2)	42.0	98	−32	95
Southern (2)	44.3	100	−36	104
Mountain-front (5, excl. Divide)	50.5	104	−30	154
Northern (1, Boulder)	50.9	97	−20	164
Divide (2)	46.7	99	−33	122
Southern (4)	50.3	104	−30	151
Plains near mountains (5)	47.7	105	−38	138
Northern (3)	47.1	105	−38	134
Southern (2)	48.6	103	−32	143
Dry plains (5)	50.4	106	−45	151
Northern (2)	48.6	103	−45	145
Southern (3)	51.0	106	−32	156
"Northern area" (8)	45.8	105	−45	131
"Southern area" (11)	49.3	106	−36	142

The number of stations for each area is given in parentheses. The mountain-front does not include the two stations of the Platte-Arkansas divide, which is so much more elevated than other parts of the mountain-front as to be much cooler. The "northern and southern areas" are respectively the northern and southern parts of the region, each extending over foothills, mountain-front, and plains.

many of the plant species are characteristic of northeastern and northwestern coniferous forest regions, are in fact southern extensions of them. The boreal character is much more evident in the higher mountains than in the foothills.

The mountain-front has the longest frostless season, the highest mean temperature, the mildest winters, and the least range in temperature extremes. Mountain-front localities are mostly comparatively sheltered; temperature inversion is common. Early spring plants flower several weeks earlier at the mountain-front than in either plains or foothills; at Boulder in spring the

season is in general 2–3 weeks in advance of that of Denver, 14 miles from the mountains.

The divide between Platte and Arkansas drainage, which should be considered in connection with the mountain-front area, has a mean temperature and frostless period intermediate between those of mountain-front and foothills areas, as it is intermediate in altitude and in vegetation.

The plains have a slightly lower mean temperature and shorter season without frost than the mountain-front area; the temperature of the dry plains at some distance from the mountains approaches that of the mountain-front more closely than that of the plains adjoining it. This difference is accompanied by a floristic one. Temperature extremes are greatest in the plains, a condition inimical to growth of woody plants.

The plains, mountain-front, and foothills in northern Colorado ("northern area") are cooler than those to the south, but the north-south differences in temperature and length of growing season due to latitude are of much smaller range and influence upon vegetation than the east-west differences due to altitude and changes of topographic character.

For purposes of comparison table III includes rainfall data for the higher parts of the mountains bordering the foothills on the west (montane zone), and for the plains of eastern Colorado bordering the region studied on the east. Annual rainfall is higher to the west, increasing with elevation, and higher also in the eastern plains, as a part of the gradual geographic increase of rainfall from the dry belt of the Great Plains eastward through the prairie region to the border of the eastern deciduous forest region. The eastern plains mark the transition from short-grass plains to the taller prairie-grass vegetation of the prairie, and are known in Colorado as "the rain belt." The driest part of the plains region lies between the rain belt and the plains near the mountains, in a zone distant from the mountains about 18–25 miles, and of a breadth 30–60 miles. It is narrowed on the west by the elevation of the Platte-Arkansas divide, and extends farther eastward in the Arkansas River Valley. It extends only a little way north into Wyoming and apparently is much narrowed on the west in extreme southern

TABLE III

RAINFALL DATA

Area	Annual	January	February	March	April	May	June	July	August	September	October	November	December
Montane zone (6) 8250–10,265	**22.58**	0.80	1.10	1.96	2.75	2.85	2.01	3.38	2.70	1.61	1.64	0.80	0.99
Foothills (10) 6890–8000	**16.30**	0.42	0.60	1.11	2.17	2.23	1.27	2.79	2.06	1.29	1.27	0.55	0.44
Northern (6)	16.75	0.42	0.68	1.38	2.26	2.88	1.47	2.20	1.90	1.29	1.31	0.47	0.49
Southern (4)	15.63	0.44	0.49	0.69	2.03	1.25	1.18	3.67	2.29	1.27	1.23	0.68	0.37
Mountain-front (13) 5069–7373	**16.25**	0.40	0.68	1.07	2.06	2.59	1.79	2.41	1.81	1.23	1.11	0.53	0.54
Northern (5)	16.95	0.46	0.68	1.48	2.64	3.11	1.56	1.99	1.29	1.31	1.29	0.55	0.52
Divide (3)	16.53	0.35	0.56	0.94	2.08	2.69	2.17	2.73	1.96	0.77	1.11	0.47	0.69
Southern (5)	15.38	0.35	0.74	0.72	1.47	2.01	1.78	2.69	2.25	1.37	0.93	0.56	0.48
Plains near mountains (6) 4985–6098	**14.36**	0.33	0.49	0.81	1.85	2.28	1.76	2.17	1.81	1.20	0.81	0.47	0.43
Northern (3)	14.22	0.45	0.51	0.97	2.02	2.70	1.57	1.87	1.34	1.05	0.90	0.43	0.44
Southern (3)	14.54	0.20	0.47	0.65	1.67	1.86	1.94	2.47	2.27	1.34	0.72	0.51	0.43
"Northern area" (14)	**16.28**	0.44	0.64	1.33	2.20	2.92	1.53	2.06	1.57	1.27	1.22	0.50	0.49
"Southern area" (12)	**15.25**	0.35	0.59	0.69	1.46	1.72	1.56	2.96	2.27	1.33	0.93	0.59	0.43
Dry plains belt (7) 3899–5400	**12.73**	0.26	0.39	0.74	1.62	2.17	1.49	2.26	1.67	0.79	0.75	0.29	0.36
Eastern plains (8) 3380–5178	**16.95**	0.35	0.53	0.76	2.01	2.59	2.58	2.89	2.06	1.29	0.87	0.52	0.52

The northern area is the aggregate of northern foothills, mountain-front, and plains; the southern area is its southern equivalent. The number of stations is given in parentheses for each area, and the range of altitude above sea-level of the several north-south zones (in feet) is also included. The rainfall figures are in inches.

Colorado and northeastern New Mexico by the lava-capped plateaus which there extend eastward from the mountains.

As for the mountain-front and adjacent foothills and plains, the first two average about the same, the mountain-front receiving slightly more rainfall in the north and at the divide than the foothills. This may perhaps be due to the fact that in the northern part of the state, as at Boulder, the rain usually comes with east and northeast winds; and since the change of elevation is greatest at the mountain-front, more precipitation might occur there than in the foothills beyond. At Boulder the more mesophytic forms of vegetation occur more frequently and in larger areas in the sedimentary rocks of the mountain-front than in the granite foothills half a mile or a mile inside the foothills. In the southern part of the state the mountain-front is drier than the foothills, as a rule. The plains near the mountains receive almost 2 inches less rain, on the average, than foothills and mountain-front, and the dry plains to the east nearly another 2 inches less.

The "northern area" (foothills, mountain-front, and adjacent plains) receives on the average about 1 inch greater rainfall than the "southern area." Coupled with the higher temperature and greater evaporation, this results in a considerably more xerophytic vegetation south of the Platte-Arkansas divide. There is little difference in the plains, but at the mountain-front, with a difference of 1.57 inches, the vegetation to the south is markedly drier.

COOPER finds, in the chaparral region of California, that very slight differences in the original physical conditions of north and south slopes result in very marked differences in vegetation. The same principle seems to apply, in perhaps a smaller degree, in a semi-arid region like the Colorado mountain-front. It appears that differences in rainfall from place to place, or from month to month, although small in absolute amount, can be critical in their influence upon vegetation distribution. The slight differences appear to represent marginal values above or below a critical point. The difference in vegetation in two areas, moreover, is not necessarily the result of climatic difference, but is a resultant of differences in soil, topography, geographic position, and vegetational history, in addition to climate. It should not be surprising, therefore, that

areas having climates not widely dissimilar, as the plains of the rain belt and the northern foothills, should have distinctly unlike vegetation.

MINIMUM RAINFALL.—One factor which seems to be partly responsible for the generally xerophytic character of the entire region studied, the plains in particular, is the wide variation in the amount of rainfall from year to year. The minima have been

TABLE IV

MINIMUM ANNUAL RAINFALL

AREA	NUMBER OF STATIONS WITH RECORDS		AVERAGE MINIMUM FOR AREA		LOWEST MINIMUM RECORDED FOR ANY STATION IN AREA	
	1893	Other years	1893	Other years	1893	Other years
Montane zone.....	—	6	—	**15.65**	16.55 Frances	**11.36** (1907) Cripple Creek
Foothills.....	4	9	—	**12.83**	**7.16** Box Elder	10.93 (1908) Cheesman
Mountain-front and divide.....	7	11	9.12	**11.91**	**7.03** Waterdale	8.76 (1890) Table Rock
Plains near mountains.	5	6	9.39	**8.91**	7.11 Fort Collins	**5.04** (1876) Cheyenne
Dry plains belt.....	7	7	8.11	**7.01**	5.40 Greeley	**3.78** (1894) Las Animas
Eastern plains.....	5	8	10.48	**10.61**	8.30 Cheyenne Wells	**6.97** (1894) Cope

Two stations within the foothills area are exceptional as to rainfall, and have not been included in the averages. These are Salida in the Arkansas Valley above the Royal Gorge, and Westcliffe in the Wet Mountain Valley. Similarly, Canyon City at the debouchure of the Arkansas, and Raton and Las Vegas in New Mexico, have been excluded from the mountain-front area. The stations with the lowest minima have been mentioned in the table. The lowest minimum in each area, whether in 1893 or in some other year, is printed in bold face. Except for Cheyenne Wells, which is remote from the mountains, all of the stations noted as having had least rainfall in 1893 are within a limited area (in the northern part of the region), which seems to have been most severely affected by the drought of that year.

tabulated for the several parts of the region from the climatic summaries of the Weather Bureau. The year 1893 happened to be exceptionally dry, and the minima for many of the stations fall in it. Dryness in other years has been of more local prevalence. It has seemed preferable to present the data for 1893 separately from that of other years. The data for 1893 are not available for all stations in each area, and so the number of stations from which data have been used is mentioned for each area (table IV). The column presenting the average minima for the several areas (minima

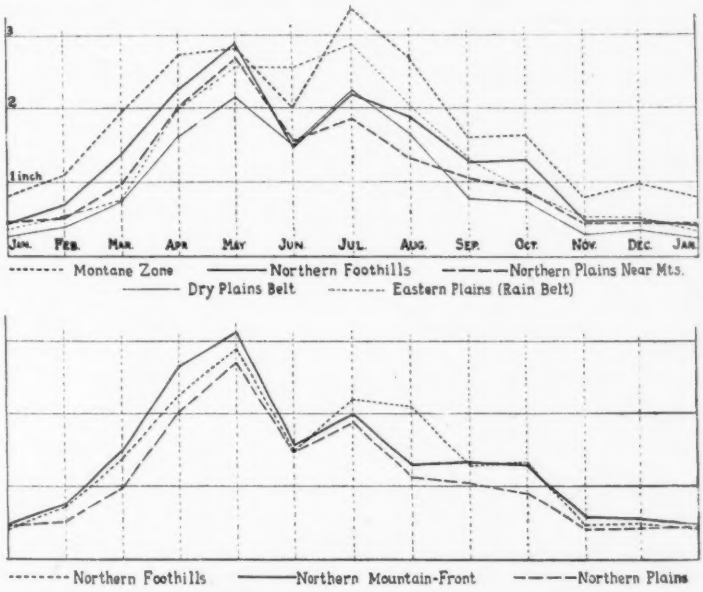
of all stations for each area averaged, excluding figures for 1893) seems to express the main fact of the table, that the rainfall reaches successively lower minima downward and eastward from the mountain zone through the foothills, mountain-front, and adjacent plains to the dry plains belt, beyond which the minima rise gradually with the gradual increase of rainfall eastward into the prairie-grass region. It appears also that annual rainfall values falling considerably below the average (as much as 4 inches below) occur more frequently in the plains than in the mountain-front and foothills areas. The well known uncertainty of farming without irrigation in much of eastern Colorado, due to frequency of very dry years, indicates further that it is not the average rainfall so much as the constantly recurring minimum which determines whether or not an area can support a cultivated or natural vegetation which is other than decidedly xerophytic.

SEASONAL DISTRIBUTION OF RAINFALL.—On the whole, precipitation during the cooler months is quite low; this is not so true of the montane area just to the west of and above the foothills. The summer rainfall is greater, but in most places distributed rather unevenly. June is thus drier than either May or July over practically the entire region. The northern area near the mountain-front receives more rain in the spring and early summer months, while the southern area receives more of its rain during late summer. This difference between north and south is of far-reaching influence upon the character and distribution of vegetation. The details of seasonal distribution of rainfall are shown in the table of averages of rainfall data, and in figs. 13–16.

The northern and southern parts of the zones at and near the mountain-front are so different as to rainfall that they cannot be incorporated in single graphs. The northern parts of the zones are selected, therefore, as the more typical. The graph for the mountain-front is omitted to avoid overcrowding, but it can be seen in fig. 14. Excluding the eastern plains, the zones have the same type of rainfall, with greatest abundance in May and July, and a decline in June. The zones are successively drier with decrease of elevation, and this is almost as true for particular months as it is for the entire year. The eastern plains have higher

summer rainfall than the plains near the mountains; the distribution is similar, except that June is as rainy as May.

The graphs for foothills and plains near the mountains are repeated in fig. 14. These zones and the mountain-front have maximum rainfall in May, with a sharp decline in June, followed by slightly greater rainfall in July. Despite its less elevated position, the mountain-front receives greater spring rainfall than the foothills.

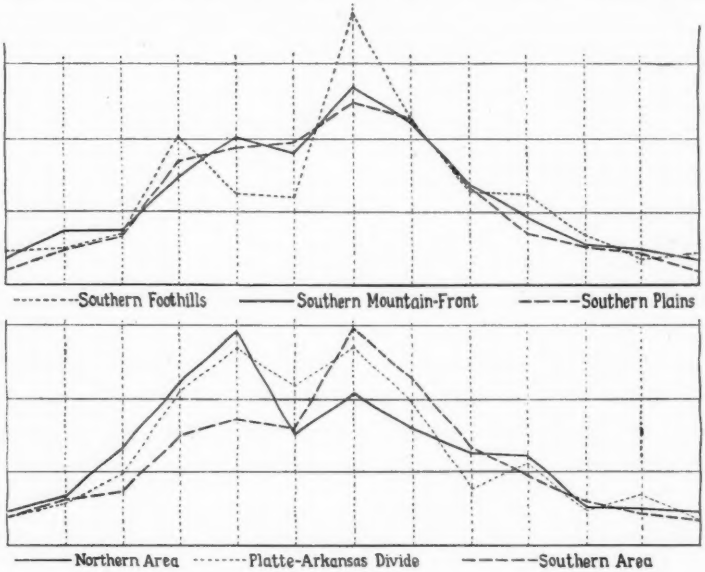


FIGS. 13, 14.—Seasonal distribution of rainfall: fig. 13, comparison of north-south zones; fig. 14, northern foothills, mountain-front, and plains.

The data for the south are not so dependable as for the north, for some of the few stations are exceptionally situated. The contrast shown with the northern area is marked, however. The rain is less abundant in spring and more abundant in July and August than to the north.

The graph shown for the "northern area" is a composite of the 3 in fig. 14, that of the "southern area" is a composite of those

in fig. 15; they contrast strongly. The northern area is characterized by the Rocky Mountain foothill type of rainfall, the southern area by the New Mexican type (WARD 19). Both of these types are described as having a single maximum, for the first in May, for the second in July-August. The northern area receives most of its rain from northeasterly winds; the southern area probably from southeasterly winds. The centrally situated Platte-Arkansas



FIGS. 15, 16.—Seasonal distribution of rainfall: fig. 15, southern foothills, mountain-front, and plains; fig. 16, northern and southern areas and divide.

divide receives rain from both directions, and has both maxima, with a higher June rainfall, partly because of its considerable elevation. Probably rain is carried from either direction past the divide, producing secondary maxima, in July in the northern area, and in April in the south.

The abundant rainfall of the divide, especially in June, forms a local rainfall type which is intermediate between that of well watered parts of the foothill zone and that of the eastern or rain-

belt plains. The divide is also cooler than most parts of the mountain-front and adjoining plains. The vegetation of the divide is likewise transitional between that of rain belt and foothills, with the more nearly mesophytic forms of grassland, and with woody plants of the foothills extending many miles eastward from the mountains.

The effects upon the vegetation of the difference in distribution of precipitation north and south of the divide are discussed in the section on geographic relations, but may be summarized briefly herewith.

TABLE V

INFLUENCE OF SEASONAL DISTRIBUTION OF RAINFALL ON VEGETATION

NORTHERN AREA	SOUTHERN AREA
The greatest rainfall is in April and May.	The greatest rainfall is in July and August.
There is greater activity of vegetation, more luxuriant growth, and greatest abundance of flowers in spring.	There is greater activity of vegetation and more luxuriant growth in late summer.
There are many spring-flowering plants from the mountains of rather mesophytic character, in mixture with plains plants in the mountain-front zone.	There is absence or scarcity of spring-flowering mountain plants, and greater prevalence of plains plants in the mountain-front zone.
Distribution of the bunch-grass association and of the less xerophytic plants, requiring a long season of continued moisture, is limited.	Distribution of bunch-grass is less restricted; there is a greater prevalence of late-flowering plants not intensely xerophytic, as some of the asters and goldenrods, etc.
The northern plains near the mountain-front flower luxuriantly in spring and early summer, but only the more xerophytic composites, etc., in late summer, in which respect the plains are more like the driest plains just east of them in late summer.	The southern plains near the mountains contain fewer spring flowers, but many long-season plants absent from the dry plains and the northern plains near the mountains are present, as the annual sunflowers. In this respect the plains are more like those of the rain belt of eastern Colorado in late summer.

It is remembered that the southern area is in general drier and warmer, with somewhat more xerophytic vegetation than the northern area, and that differences in vegetation due to this cause must be distinguished as well as possible from those due to different distribution of rainfall.

Evaporating power of the air has not been subject to geographic-statistical treatment, since there are no data. It was beyond the scope of the present study to have attempted instrumental investigation on a scale large enough to be of value. There seems to be little doubt that, as a geographic factor *in regions of continental climate*, evaporating power of the air is of about the same indicator value as rainfall. It varies geographically about as does rainfall, in inverse ratio, since evaporating power is, in large measure, a function of rainfall. This same inverse ratio seems to hold in seasonal distribution as well as geographically. This may be seen from the graphs of WEAVER (**20**), and from data obtained by COOPER in a study of chaparral in California.

As a local factor evaporation is separately treated in the discussion of local distribution of vegetation.

For further discussion of the climatology of Colorado in relation to vegetation the reader is referred to the articles of SHANTZ (**15, 16**), RAMALEY (**12**), and ROBBINS (**13, 14**). Data may be had from the bulletins of the United States Weather Bureau, Colorado College, the Agricultural Experiment Station at Fort Collins, and the Bureau of Plant Industry.

Local distribution of vegetation

PHYSICAL FACTORS.—Local physical conditions affecting plant distribution are those concerned with *substratum* and *soil;* with *topography*, especially *local position* with respect to surroundings, and *slope* of surface, as regards both steepness and direction of exposure; and with *local variation in atmospheric conditions*, as controlled primarily by topography. The variability of these factors within the region is great, and their interactions are complex. Descriptions of the soil, topography, atmospheric conditions, etc., of the different parts of the region are scattered through both systematic and regional sections of this study, and a lengthy discussion at this point would be out of place. A few references to other parts, and certain incidental comments, may here be made.

The character of the substratum, and some of its influences in determining soil conditions and topography, are indicated in the

account of the sedimentary area. The contrast between the granite soil of the foothills and the soil of sedimentary origin lying just outside, with its slight selective action on flora and vegetation, has also been noted. Other mentions of soils, especially as regards soil texture, are scattered.

Topography is systematically treated for particular regions and smaller areas by dividing each type of topographic complex into topographic areas or habitats; with each type is correlated the particular plant community or the several communities which accompany it. In the regional section will be found similar analyses of the cuesta, high mesa, mesa-terrace, and flood-plain complexes. Particular physical factors controlled by local position and by slope are mentioned in a former article (**18**).

Atmospheric factors vary locally in this region to a probably not very great extent, but even slight differences may be critical, as has been found by COOPER in the California chaparral. The factor of greatest influence upon plant life, and the one most readily measured, is the evaporating power of the air, the value of which represents the resultant of several contributing factors. Local distribution of evaporating power is believed to be controlled primarily by differences in topography, and secondarily by differences in vegetation-cover. That is to say, flatness of the land surface makes for comparative uniformity of exposure to wind and sun; hilliness causes diversity of exposure. Local water or wet-soil surfaces may lower evaporating power by contributing much water vapor to the air. Topography thus determines the *original* local distribution of evaporating power. This original local distribution is modified by vegetation-cover. In flat country the uniformity is changed. Low and open vegetation lowers evaporating power at the ground surface only slightly, but mesophytic closed forest lowers it very greatly (GATES **3, 4**). In hilly country in not too humid climates the originally protected ravines and shaded or wind-sheltered slopes may develop mesophytic vegetation which still further lowers evaporation, while the originally exposed slopes and summits usually remain xerophytic. Thus, in the mountain-front region here considered, primary environmental differences

due to topography may rather thoroughly control vegetation distribution. In such cases the reaction of vegetation-cover upon local evaporation conditions may merely heighten the original topographically determined contrast between protected and exposed habitats. Topography governs local vegetation distribution through the mediative influence of a number of physical factors, of which evaporating power is one. Depending as it does upon several other factors, evaporation forms a convenient index of habitat, but is not in itself the basic controlling condition. For these reasons the writer has subordinated the influence of evaporating power upon local distribution to that of topography.

The sudden change of elevation at the mountain-front is a topographic condition affecting evaporating power. At many places the hogbacks, mesas, and outer slopes receive no direct sunlight during several hours before sunset, being shaded by the higher slopes immediately to the west. This contributes to the comparative mesophytism of certain mountain-front stations where the descent from foothills to plains is more than ordinarily abrupt.

Direction of exposure affects local atmospheric conditions and vegetation in many easily observed ways. Cloudiness and showers occur on summer afternoons much more frequently than in the mornings, as RAMALEY has noted. East-facing slopes are thus likely to be drier than west-facing slopes (the latter are less frequent east of the range-crest). As would be expected, the difference between north- and south-facing slopes is considerable, the latter being more exposed to sun and conditions favoring rapid evaporation, and with sparser, more xerophytic vegetation. In open parts of the foothills where slopes are quite gentle the north-facing slopes are not sufficiently sheltered from sun and wind to differ in vegetation from the south-facing slopes in any marked degree. Steep north slopes, or both sides of steep and narrow ravines which run down to the north, however, are quite mesophytic. In different parts of so large a territory the combinations of contrasting vegetation of north and south slopes would be expected to vary, and a few of them are listed herewith by way of illustration.

TABLE VI

EFFECTS OF DIRECTION OF SLOPE UPON LOCAL DISTRIBUTION

Locality	Vegetation of south-facing slope	Vegetation of north-facing slope
Poudre foothills	Grassland	Scattered rock pine, with more mesophytic vegetation infrequent
Foothills near Boulder	Grassland, rock pine, mixed shrub	*Pseudotsuga*, canyon forest, rock pine, mesophytic grassland
Poudre mountain-front	Grassland	*Cercocarpus*, with very scattered rock pines in rocky places; grassland in fine soil
Mountain-front near Boulder	Grassland, mostly	Grassland with rock pine, mixed shrub, etc.
South of Golden, mountain-front	Grassland and *Cercocarpus*	Grassland with scattered rock pine and mixed shrub
Perry Park	Oak and grassland	Rock pine and *Pseudotsuga*
Palmer Lake	Oak	*Pseudotsuga*
Southern mountain-front in general	Pinyon-cedar, dry grassland, and scattered oaks	Closer and taller oak growth with rock pines

FACTORS OTHER THAN PHYSICAL CONDITIONS OF HABITAT.—If the physical conditions which determine the habitat and all their interactions and variations were fully known, however, the local distribution of plant communities as observed would only partially be explained. Within even a very small part of the region studied correlations between physical habitats and vegetation-types must not be too closely drawn. The rock pine, for example, grows in any soil or on any slope; its presence or absence in any particular situation is not alone a matter of physical conditions there and then operative. Local distribution of vegetation-types in these partly unstable and locally very diverse situations depends also on at least three other sets of conditions: (1) range of toleration, in individual species or groups of species, of variation of physical conditions; (2) local historic factors, physical and vegetational, which have been operative in any given spot (these often cannot be determined); (3) accident of seed distribution and germination. For these reasons it seems best to characterize the vegetation-units, in most cases, from the vegetation itself rather than from habitat. There can be no question

that, in general, local variation of present physical conditions of the habitat governs to a considerable degree the distribution of plant communities, but the need of at least recognizing these other sets of factors should be emphasized. It must be further seen that, in the invasion of a new habitat, representatives from more than one plant community can be successful in establishing themselves, resulting in *mixed vegetation-types*. In fact, probably the greater part of the area studied is occupied by mixed associations or *mictia* (CLEMENTS). Even areas of established vegetation are usually open enough to permit the continual ecesis within them of new plant immigrants from quite different communities. This diversity is likely to be relatively enduring, for plant competition usually does not here operate to exclude all but a single type of dominants. The opposite relation between plants, which may be called accommodation, is as greatly in evidence. The control exerted by vegetation upon the physical environment is slight over the generally xerophytic mountain-front region.

A second factor contributing to the mixed effect is the frequent extremely local variability of physical conditions within the habitat. This might be called *mosaic variability*, and its effect a *mosaic mixture* of vegetation-types. The influence of large surface rocks partly imbedded in fine soil, allowing the growth of comparatively mesophytic plants in a rather constant interspersal with xerophytes over a considerable area, may be cited as an example.

Vegetation-types and their distribution

Since the plant communities have been described separately in the two articles preceding this, their systematic characterization here may be condensed very considerably. A tabular view of the communities, giving some idea of their general character and of their distribution in the main geographic divisions of the region studied, is shown in table VII.

Some of the more important features of the particular associations may now be noted. Details and references to other accounts may be found in the articles preceding. The general appearance of certain vegetation-types may be seen in fig. 17.

Lichen association.—Lichens, especially *Rinodina*, *Lecanora*, and *Parmelia conspersa*, partly cover the dry rock surfaces, especially granites in the foothills and the craggy outcrops and loose surface rocks of the mountain-front. Rock exposures are infrequent in the plains proper.

TABLE VII

CONSPECTUS OF ASSOCIATIONS

	Foothills	Mountain-front	Plains
Thallus vegetation	Lichen association	Lichen association	(Lichen association)
Grassland			
Extensive, climatic	Foothills grassland	Mixed short-grass	Short-grass
Local, edaphic			
Xerophytic	.....	Wheat-grass *Stipa-Aristida*	Wheat-grass *Stipa-Aristida*
Less xerophytic	Bunch-grass, plus a foothills element	Bunch-grass	Bunch-grass
	Mesophytic grassland	Prairie-grass	(Local, infrequent, prairie-grass-like communities)
	forest herb type		
	meadow type	meadow type	(meadow type)
		mixed type	(mixed type)
Primitive	Foothills primitive grassland	Primitive grassland	Primitive grassland
	Artemisia frigida consocies	*Artemisia frigida* consocies	*Artemisia-Gutierrezia* consocies
		Primitive bunch-grass	Primitive bunch-grass
Shrub vegetation			
Xerophytic	*Cercocarpus* association	*Chrysothamnus-Sarcobatus* association *Cercocarpus* association	*Chrysothamnus-Sarcobatus* association
Xerophytic to mesophytic	Mixed shrub association	Mixed shrub association	(Local shrub communities)
	Arctostaphylos *Ceanothus* association *Symphoricarpos*	*Symphoricarpos*	(*Symphoricarpos*)
Tree vegetation			
Coniferous			
Xerophytic	Pinyon-cedar association	Pinyon-cedar association	
Less xerophytic	Rock pine association	Rock pine association	
Relatively mesophytic	*Pseudotsuga* association	(*Pseudotsuga* association)	
Deciduous			
Xerophytic to mesophytic	Oak association	Oak association	
	Populus-Salix association	*Populus-Salix* association	*Populus-Salix* association
Relatively mesophytic	Canyon forest (Aspen association)	Canyon forest	

Associations with equivalent or similar representation in plains, mountain-front, and foothills areas are shown on the same horizontal line. Very local or poorly developed representation of a community in a particular zone is indicated by parentheses.

Mixed grasslands and short-grass.—The shallow-rooted short-grasses, *Bouteloua* and *Bulbilis*, dominate the compacted fine soil surface of most of the plains, as the well known short-grass association. *Bouteloua* alone, with admixture of plants of different physiological and geographic character, is the important element of dry

FIG. 17.—Distribution of vegetation in typical northern mountain-front area (outlet of Gregory Canyon, near Boulder): habitats and vegetation-types distinguishable are: 1, craggy exposure of Fountain sandstone; 2, rock talus, with beginning of primitive grassland; 3, stabilized slope with primitive grassland; 4, mixed grassland, in places approaching mesophytic type, mostly on northwest-facing slope; 5, more nearly xerophytic mixed grassland, with bunch-grass and ruderal elements on northeast-facing slope; 6, *Symphoricarpos*; 7, mixed shrub; 8, canyon forest; 9, *Populus angustifolia* stream-side community; 10, rock pine; 11, *Pseudotsuga*, in scattered growth, including rock pine and other components, on north-facing slopes of Green Mountain.

grassland in the débris-covered soil of the mesas and outwash-plains of the mountain-front (short-grass mixed association). The foothills mixed grassland, very similar to the mixed short-grass, is typical over the coarse surface of the granitic foothills.

Wheat-grass.—This taller but also shallow-rooted grass, *Agropyron Smithii*, dominates areas of loose clay in the mountain-front and plains. Its ecological character is not well understood.

Stipa-Aristida association.—These tufted xerophytic grasses of coarse soil occur frequently but not extensively, together or singly, with other rather deep-rooted plains xerophytes.

Bunch-grass.—Tufted perennial and deep-rooted grasses, depending on continued moisture, such as *Andropogon scoparius*, *A. furcatus*, *Sorghastrum nutans*, etc., are notable through most of the prairie region, almost absent in dry plains, but abundant in the rain belt of eastern Colorado; at the mountain-front and in the foothills, scatteringly in the north, but very frequent at the Platte-Arkansas divide and southward into New Mexico. In the foothills there are grasses of similar habit which mingle with the prairie bunch-grasses.

Mesophytic grasslands.—Mesophytic herbaceous growths are made up partly of prairie plants and partly of Rocky Mountain forest plants. The latter element is very considerable in occasional foothill ravines. Meadow growths of both foothills and mountain-front, in moist soil, with showy flowering plants like *Delphinium*, *Cerastium*, *Castilleja*, *Orthocarpus*, etc., are conspicuous in early summer, but not very frequent. The mountain-front in many places shows a mixed grassland much like that of eastern prairie, which has been called western prairie-grass. It has plants of the mixed short-grass, with components from bunch-grass and eastern prairie or forest border, with some foothills mesophytes, and a few plants characteristic of the mountain-front, like *Stipa viridula*.

Primitive grasslands.—Early stages of grassland developing in areas recently bared, or remaining for long in loose shifting slopes, are frequently seen. Prostrate plants with heavy taproots (rosette plants) are common. Gravel-slides in the foothills and dry stony crests of mesas, buttes, and ridges in the plains and mountain-front are the typical habitats. The *Bouteloua hirsuta*

community; 19, rock pine; 11, *Pseudotsuga*, in scattered growth, including rock park and other components, on lower facing slopes of Green Mountain.

and the *Artemisia frigida* consocies may be mentioned specially. The last is closely allied to the *Gutierrezia-Artemisia* association of the plains, very widespread, and continuing, at the expense of short-grass, with heavy grazing. In mountain-front and plains the primitive bunch-grass association, with *Panicum virgatum*, *Sporobolus cryptandrus*, *Stipa Vaseyi*, *Eriocoma*, etc., occupies sandy or loose-soil habitats recently disturbed.

Chrysothamnus-Sarcobatus association.—The shrubby composite, *Chrysothamnus* (rabbit-brush), and the chenopodiaceous greasewood occupy loose soil, mostly alkaline areas, on certain slopes in the mountain-front, and are particularly abundant in stream-bottoms in the southern plains.

Cercocarpus association.—Mountain-mahogany, of the rose family, is the only dominant in the open shrub growth of the mountain-front and outer foothills, in very dry exposed situations and usually stony soil. In the interstices between shrubs are plants of primitive grassland or mixed short-grass.

Mixed shrub association.—This is a heterogeneous assemblage of shrubs, ranging from xerophytic, like *Rhus trilobata*, to relatively mesophytic forms, like *Crataegus coloradensis*, in sheltered situations. The same species range through a variety of habitat conditions, and may form a community either as shrubs or trees. The mixed shrub grades into the canyon forest.

Arctostaphylos association.—The well known and widespread bearberry forms its characteristic mats in the foothills, mostly on compacted gravelly floors. It is more abundant in the upper foothills, in open places among the scattered pines. Its congener, *Juniperus communis sibirica*, is present but infrequent.

Ceanothus association.—*Ceanothus Fendleri* forms low matlike ground-cover in the lower foothills, similar to that of *Arctostaphylos*, though it is not evergreen, is of more southerly distribution, and ranges into drier and more exposed habitats. It favors the establishment of seedling mesophytes, and plays a part in revegetation of burned areas.

Symphoricarpos association.—The buckbrush, as it is called, occupies moist fine soil, and invades grassland in the mountain-front and foothills, as well as in the eastern prairie, in favorable

situations such as draws and seepage areas of slopes. It in turn is frequently displaced by taller woody vegetation.

Rock-pine association.—Pinus scopulorum is the important tree of the foothills. It ranges into very variable habitats, and is structurally variable in accordance. It forms infrequent close stands, but in most places is scattered, the ground between the trees being occupied by foothills mixed grassland, *Ceanothus*, *Arctostaphylos*, etc. It is frequent in rocky crests, etc., in the mountain-front, except in the south, where it is commonly replaced by pinyon. It extends very locally into the plains in broken country, on butte-crests, etc., and on the elevated Platte-Arkansas divide.

Pinyon-cedar association.—Pinus edulis and *Juniperus monosperma* are important xerophytic conifers of the southern mountain-front and lower foothills north to the Garden of the Gods, and extending into the southern plains on mesa-crests, canyon-walls, and bluffs of broad valleys. The soil is usually rocky or gravelly. The trees are low and rounded, and do not form a closed assemblage.

Pseudotsuga association.—Pseudotsuga mucronata forms the mesophytic or relatively mesophytic coniferous forest of the region, and is confined to sheltered ravines and steep north slopes in the foothills. It is infrequent at the mountain-front.

Oak association.—Small trees of the white-oak group, of uncertain taxonomic affinity, form dense copses or open woods in the lower foothills and in the mountain-front about as far north as Platte Canyon. In places grazing destroys the oak slowly and allows increase of grassland. The undergrowth of mesophytic oak areas is much like that of the canyon forest.

Populus-Salix association.—In stream-side areas of the foothills *Populus angustifolia* and 4 or 5 common willow species are frequent. Outside the mountains *Populus Sargentii*, and in the south *Populus Wislizeni*, replace the narrow-leaf cottonwood. Cottonwoods extend eastward into the plains for many miles along watercourses.

Canyon forest.—The deciduous trees of the foothill canyons and of ravines, etc., in the mountain-front, include *Alnus tenuifolia*, *Betula fontinalis* (these two common along mountain streams),

Amelanchier alnifolia, *Prunus pennsylvanica*, *P. americana*, *P. demissa*, *Crataegus coloradensis* et spp., *Robinia neomexicana* (in the south only), *Acer glabrum*, and *A. Negundo*, with a few others. A few shrubs are present and a variable undergrowth, with one typical aspect of *Viola canadensis* Rybd., *Hydrophyllum*, and *Galium*. A *Ligusticum* is very abundant in places.

Aspen association.—*Populus tremuloides* is restricted, in all but the highest parts of the foothills, to relatively mesophytic ravines. It does not come up abundantly following burning of the pine forest, as is true in the higher elevations and farther north.

EASTERN ILLINOIS STATE NORMAL SCHOOL
CHARLESTON, ILL.

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ON NITRIFICATION[1]

III. THE ISOLATION AND DESCRIPTION OF THE NITRITE FERMENT[2]

AUGUSTO BONAZZI

(WITH PLATE XIV)

Introduction

As a part of the physiological investigations upon nitrification carried on in this laboratory, the isolation of pure cultures of the nitrite-forming organisms became a necessity. Since difficulties in the isolation of these organisms have been encountered by many workers in the field of soil bacteriology, and since no accurate description of the organisms of nitrification from North American soils has been published as yet, it was deemed advisable to describe the organisms responsible for the formation of nitrites in the Ohio soils and the methods used in their isolation.

The following contribution, which is the result of a long period of study, is here given to describe an organism, capable of forming nitrites from ammonia, isolated in a pure state from Wooster soil after many unsatisfactory attempts.

Historical

In 1890 JORDAN and RICHARDS (4) in Massachusetts stated that they had isolated a nitrifying organism which was capable of oxidizing ammonia salts to nitrates when grown in solutions free of organic matter. The dilution method was the one relied upon by these investigators for obtaining pure cultures. Their description of this nitrifier is here reproduced.

[1] Contribution from the Laboratory of Soil Biology, Ohio Agricultural Experiment Station.

[2] The first paper of this series dealing with the subject of nitrification appeared under the title "Preliminary observations" in Ohio Agric. Exper. Sta. Technical Bull. 7. 1915. The second paper under the title "Intensive nitrite formation in solution" appeared in Jour. Bacteriology 1918. Thanks are due Dr. E. R. ALLEN, in whose laboratory this work was undertaken, for kind advice and criticism.

The bacilli are short, of a slightly oval shape, and vary from 1.1 μ to 1.7 μ in length; they are about 0.8–0.9 μ broad. They are grouped characteristically in irregular clumps and are held together by a jelly-like material. Each aggregation is indeed a typical zooglea. The aggregations of bacteria were found chiefly in the bottom of the flasks, as was also the case with the organism described by WINOGRADSKY. . . . . On one important point there appears to be a difference between our results and those reached by the above mentioned investigators. The organism discovered by them oxidizes ammonia to nitrite, but carries it no further. Our flasks give complete oxidation to nitrate. . . . . We are not even prepared to say that there may not have been a mixture of two or more species in our flasks, all agreeing closely in morphological characters, and in giving no growth on gelatin, but differing in important physiological respects.

This statement makes it quite clear that probably their cultures were a mixture of the two forms isolated and separated by WINOGRADSKY (**11**). No lengthy description of the organisms isolated by the Russian investigator is here necessary, and a summary review of his findings (**12**) will suffice. The nitrite-forming organisms from different parts of the world were divided by WINOGRADSKY in two genera and several species as follows: *Nitrosomonas* (*N. europeae* and *N. javaniensis*), from the Orient; and *Nitrosococcus*, from the Occident. *Nitrosomonas* received by far the greatest attention from WINOGRADSKY, while *Nitrosococcus*, which is most important to American economy, he only incompletely described. The soils from which WINOGRADSKY isolated his *Nitrosococcus* were from Campinas (Brazil), Quito (Ecuador), and Melbourne (Australia).

Samples of North American soils were not studied, and it is surprising that no description of organisms from such soils has been attempted since the time of the discovery of the active agents of nitrification. It is true that JORDAN and RICHARDS gave a description of the sewage organisms they were working with, but their description does not conform to the one given by WINOGRADSKY of the South American organisms. It is evident, therefore, that, were it only from a geobotanical standpoint, the description of the organisms from the Northern Hemisphere presents some importance.[3]

[3] The investigations reported by OWEN, WM. L. (The effect of carbonates upon nitrification. Georgia Exper. Sta. Bull. 81. 1–42. 1908), should not be overlooked in this connection. Unfortunately it must be admitted that the photographic reproductions of the organisms which he found in his flasks remind us only of a mixture of

The organism from Quito soils had, according to its discoverer, the following characters: a large coccus 1.5–1.7 μ in diameter, appearing larger in the living state than in the stained preparations. According to WINOGRADSKY this was probably due to a thick gelatinous membrane which did not stain or become invisible on desiccation. Typical zooglea, as those of *Nitrosomonas*, were never found, and the motile stage was never observed in liquid cultures of this organism. Corresponding to this behavior in solution, the colonies on silica jelly were only of one form, and were never seen to simulate the "clair colonies" of the *Nitrosomonas*. Surface colonies had the appearance of a yellowish liquid, and like the deep colonies were also made up of free cells. The organisms from Campinas and Melbourne showed the same characters, but were only different in size from the Quito organism, the Campinas coccus attaining a size of 2 μ in diameter, the Melbourne organism not quite 1.5 μ in diameter (a little smaller than the other two, WINOGRADSKY **12, 13**).

From this cursory review of the descriptions of the organisms it is evident that little is known, especially with regard to their cultural characters. A footnote in WINOGRADSKY'S paper (**12**) describes a peculiar linking of the cells of the Campinas organism which the author only observed once, and was not therefore in a position to study carefully. It should be mentioned also that this same Campinas organism gave a "trouble sans motilité" which WINOGRADSKY could not explain.

Criterion of purity

One difficulty encountered in the present work was the establishment of a criterion of purity, a standard sufficiently accurate to allow its general acceptance. The words "pure culture" in bacteriological literature are used to indicate such a culture as is made up completely or almost entirely of cells of the same type,

various ubiquitous bacteria, which were not active in nitrification. The actual nitrite and nitrate production in the cultures studied by OWEN was so slight, to justify their being considered non-nitrifying cultures, that this fact, together with the heterogeneous bacterial contents, points to the possibility that he might not have possessed pure cultures of nitrifying organisms.

showing within the limits of individual variations in the same species the same physiological and morphological characters. Although theoretically a "pure culture" is that culture originated monocytogenetically, in practice it is seldom obtained. True pure cultures are only possible when the development of one single cell into a colony is controlled directly by microscopical observation; in ordinary technic this is not done. Although these requisites are necessarily of the same importance when "pure cultures" of nitrite- and nitrate-producers are desired, the term "pure culture" of nitrifying bacteria does not convey this same criterion of "absolute purity."

The simple fact that WINOGRADSKY found the nitrate- and nitrite-formers of different lands to possess in common the character of not growing in bouillon, in spite of their morphological differences, and that he made of this a criterion of purity, is enough to show the misleading interpretation given to the term "pure culture." The criterion of purity formulated by WINOGRADSKY (**12**) is as follows: "Introduce a loopfull of a nitrified culture in ordinary bouillon and keep at 30° C. during 10 days; at the end of this time the bouillon must not show turbidity. The purity of the nitrifying organisms is then proven."

That this criterion of purity is rather indefinite is shown by the following statement from JORDAN and RICHARDS, who, discussing the purity of some of their cultures, state that "we are not even prepared to say that there may not have been a mixture of two or more species in our flasks, all agreeing closely in morphological characters, and in giving no growth on gelatin, but differing in important physiological respects." OMELIANSKI (**6**) states that "after renewed ammonia additions it is necessary to control the purity by microscopical examinations as well as reinoculation in bouillon."

Since WIMMER (**9**) found a culture of nitrifying organisms to prove pure on bouillon of one reaction, while this same culture proved impure when tested on bouillon of a more alkaline reaction, the author has adopted in his work with nitrite-formers the following cardinal points which form the basis for his criterion of the purity of a culture: (1) the culture must be in full nitrification

before any attempt to determine the purity by the bouillon method is made; (2) the bouillon used in testing for purity should be of an alkaline reaction; better results would be obtained if the testing were made in bouillon of different reactions; (3) the time limit necessary for absolute reliability for the growth in bouillon should be fixed at 10 or more days; (4) the inoculum used in testing for purity by the bouillon method should be as large as permissible by ordinary technic; (5) microscopical examination must reveal a picture uniform within the limits of individual morphological variation in the species and within the different phases of the same organisms, provided such phases are established as correct.

A study of the growth of different organisms on the same medium and the description thereof is often relied upon as a diagnostic method. At best this method is unsatisfactory and of limited application. This is plainly shown by the fact that we cannot attempt to compare, on the same basis, the ordinary saprophytic and parasitic organisms with such organisms as will not grow on the media used in ordinary laboratory practice. The known organisms of the latter type are not numerous at present, but doubtless they are quite abundant in nature. The nitrite-formers of WINOGRADSKY are to be classified among the latter, together with the not less peculiar *B. oligocarbophilus*, *B. pantothropus*, and some organisms of the oligonitrophilus, sulphur, and iron groups. In the case of these organisms a study of their morphology in a few special media will lead to more accurate and reliable results than any attempt made to grow them in bouillon, gelatin, or agar of the ordinary composition.

Having presented the description of the South American nitrite-formers, and the criteria of purity followed in the present work, a description of the organism isolated to comply with these rules, from a North American soil, will be given after a discussion of the isolation technic.

Experimental

After establishing nitrification in solution by means of a small soil inoculum, the growth of the organism concerned was stimulated by continued additions of new doses of ammonium sulphate, new

ammoniacal salt being added only if the culture showed no ammonia reaction when tested with Nessler's reagent. From these enrichment cultures new cultures were started in solution with small inoculi. The culture solution used in all this work was the one recommended by OMELIANSKI (**6**), of the following composition: H_2O, 1000 cc.; $FeSO_4$, 0.4 gm.; $MgSO_4$, 0.5 gm.; K_2HPO_4, 1.0 gm.; NaCl, 2.0 gm.; $(NH_4)_2SO_4$, 2.0 gm.

Filtration of the solution was deemed unnecessary, since the addition of $MgCO_3$ milk after sterilization would make the practice useless. Growth was not impaired by preliminary filtration of the medium. After several transfers in solution, attempts were made at the isolation of pure cultures by plating in ammonium sulphate washed agar. Two consecutive platings in this medium

TABLE I

Soil	0	Silica jelly plates	63
Solution	19	Solution	66
Solution	24	Silica jelly plates	71
Washed agar plates	34	Solution	76
Washed agar slants	40	Solution	84
Washed agar plates	50	Solution	86
Solution	59		

gave cultures which did not fulfil the requirements of the "criteria of purity." It was only after 3 consecutive platings in a silicic acid jelly medium (**6**) that cultures were obtained which proved pure to the criteria. The genealogic succession of the cultures is shown in table I, where the series number accompanies the description of the medium used in each generation studied.

It was only a culture of series 86 in solution that, when inoculated in bouillon of a +1 per cent and a −1 per cent reaction, gave no growth whatsoever, either before or after the 10-day period had elapsed. Microscopically no foreign forms were seen, and a perfectly pure culture was indicated by this test. Unfortunately, after this culture was obtained it was observed that its action was relatively slow, and in subsequent transfers the inoculi used were very large, 1 or 2 cc. Notwithstanding these precautions, after the cultures had been transferred once or twice again they

gave no more the characteristic nitrite formation. The genealogic succession is represented in table II.

Tests made in bouillon (of a + and − reaction) proved cultures of series 90 and series 94 to be absolutely pure. Cultures of series 86 were inoculated with 1 cc. of the mother culture, those of series 88 with 1 cc., those of series 90 with 1.5 cc., those of series 94 with 2.5 cc., and those of series 101 with one large loop of such a shape that it contained 2–3 drops of solution. The reaction of cultures from series 94 was questionable, and microscopic examination of some cultures of this series showed the organism to be very slow growing, so slow in fact as to allow a contamination to enter during the manipulations subsequent to the first test for purity. The nitrite formation of culture 101 was nil after nearly a month, and its cellular contents nil. That the loop used in this

TABLE II

Solution	86	Solution	94
Solution	88	Solution	101
Solution	90		

case was large enough for a successful inoculation, provided the mother cultures were growing well, is proved by the thousand other successful inoculations by this method.

The characters of the organisms isolated during the preceding series of generations are described later. Although these organisms in the pure state tended to lose their nitrifying power when cultivated in solutions at rest, by cultivating them in ignited soil, to which the ordinary OMELIANSKI solution and magnesium carbonate were added, it was possible to stimulate their action considerably. The cultivation of these same organisms in solutions undergoing a slow rotary movement and constant aëration proved them to possess a very strong nitrifying power. Organisms which were slowly losing their power of nitrification in the ordinary laboratory condition, as they approached a state of purity, were soon made to increase this power, up to an intensive nitrification, by appropriate means (BONAZZI 2).

Cultures in solution

Macroscopic examination of young solution cultures reveals no indication of bacterial growth, and it is not until much ammonia has been oxidized to nitrite that any macroscopic growth is apparent. By observing the bottom of the culture flask 30–40 days' old an inconspicuous slimy deposit is visible which is easily dispersed by shaking. Before this point is reached no clouding or movement of the solution is visible, such as the "trouble" imparted to the solution by the "monad stage" of the European organisms. In fact no distinction can be drawn between the inoculated and non-inoculated flasks incubated for the same period of time. This similarity is maintained throughout the life of cultures which have been kept in this laboratory for over 2 months. No surface growth is visible, even when the cultures have attained very old age. Two cultures, which had nitrified 74.41 and 48.10 mg. of ammoniacal nitrogen while at rest, showed no surface growth whatever. No motility can be observed in the cultures, and this is in conformity with the behavior of the South American cultures described by WINOGRADSKY. In all the work with solutions at rest we have adopted the use of 20 or 25 cc. of solution in 250 or 300 cc. Erlenmeyer flasks, since this depth of solution furnishes a relatively good aëration.

Cultures on solid media

Several solid media have been tried in this laboratory in the hope that a satisfactory method could be found which would be advantageous to the speedy growth of the organism of "nitrosofermentation." Among others there were tried the paper pad method and the gypsum block method of OMELIANSKI (**6**), the magnesium carbonate block method of PEROTTI (**7**), the magnesium carbonate and ammonium-magnesium-phosphate block method of MAKRINOFF (**5**), the ammonium sulphate washed agar method of BEIJERINCK (**1**),[4] the silicic acid jelly method of STEVENS and

[4] The method of BEIJERINCK was also modified so that the washed agar only came in contact with the salts a few minutes before inoculation. This was accomplished by incorporating, just before plating, the necessary quantity of salts dissolved in 5 cc. of water with 5 cc. of a melted washed agar jelly, mixing thoroughly, inoculating, and plating. The action of the salts on the agar at high temperatures was thereby avoided.

TEMPLE (**8**), and the silicic acid jelly method of WINOGRADSKY (**10**). By far the best and most reliable results were obtained with WINOGRADSKY'S silicic acid method, which has now been adopted in this laboratory as the best among all those tried. When an impure enriched culture is inoculated in silicic acid jelly plates superficially, very little visible growth takes place. The point of inoculation only assumes a perlaceous aspect and does not change with age.

When the inoculum is incorporated with the nutritive jelly and incubated at 30° C., no growth is visible before 11 or 12 days have elapsed from the time of inoculation. It is only after this period that small colonies are visible to a magnification of 75 diameters, barely distinguishable in the thick mass of crystals formed in the plate. After the lapse of a few days more the colonies reach a size of $\pm 224 \times 160\,\mu$; when observed by transmitted light they have the appearance of small yellowish masses surrounded by a colorless halo, which is due to the solution of the $MgCO_3$. This characteristic may be utilized as a means of differentiation in the identification of the colonies (fig. 1). The colonies have at first diffused outlines, and slowly take on a more definite form, their appearance being well shown in figs. 2 and 3. They never assume a hard consistency, remaining always soft. Colonies of 1 mm. diameter have been obtained by renewing the $(NH_4)_2SO_4$ in the plates when necessary, by the method recommended by OMELIANSKI.

Hanging drop cultures

Hanging drop cultures show no motility, even when the material is taken from mother cultures which are undergoing at the time a strong nitrification (figs. 7 and 8). Material prepared for microscopical observation from cultures undergoing intensive nitrification on a klinostat (BONAZZI **2**) only showed a slow vibration of the cells, easily ascribable to Brownian movement.

Microscopical aspect of organism

In the beginning of the investigation the solution cultures were searched for any growth which might resemble the typical zooglea or the typical monad forms described by WINOGRADSKY

for the organisms of the Old World. Failing in the search, attempts were made to find any organism which, by its constant abundance in the cultures, might prove to be the principal type. On account of the slow growth of the organisms of nitrosofermentation in the ordinary laboratory conditions, it was not until nearly pure cultures were obtained that I observed, mixed with and imbedded in the salt deposit, a large coccus form, much resembling the one described by WINOGRADSKY as peculiar to South American soils. The strong "ferment power" of this organism had aided it in escaping attention in impure cultures. These megalococci are shown in fig. 6. They are large, $\pm 1.25\,\mu$ in diameter, and of a slightly irregular roundish form. Some are occasionally found which appear to have a triangular section, but closer observation reveals them to be clumps of smaller cells arranged so as to simulate a tetrahedron.

The microscopical examination of material from cultures in full nitrification, answering to the criterion of purity, is the most instructive. Fig. 5 shows the appearance of the megalococci at this time; they are composed of a thick gelatinous mass in which are imbedded small granules. Very often seemingly bipolated bodies are imbedded in this jelly, but on closer examination these polar bodies appear to be, not small cocci, but diplococci, the true living active units (figs. 4, 5). Material from intensive cultures, observed fresh in strong Meissner solution, showed these structures very plainly stained differentially and larger than in the dried preparations, since on drying the gelatinous mass seems to lose its thick structure. This gelatinous coat has a thickness that equals the diameter of the cells imbedded in it, and it takes on a bluish tinge in iodine, while the imbedded cells stain golden yellow in the same reagent.

When the cultures are in full and strong nitrification, the megalococci give rise to the small cocci which we will name β. The latter are clearly shown in fig. 5. These small β forms, which were at first imbedded in a thick gelatinous mass, forming the large α cocci, are set free and begin independent life, leaving the empty sheaths which are occasionally to be seen in stained preparations. Some of the β forms have been observed to take up a

gelatinous coating and revert to megalococci. This cycle recalls a little the cycle followed by the organisms of Java soils, as related by WINOGRADSKY (**12**, figs. 10, 12).

The staining methods adopted in this study are similar to the methods recommended by WINOGRADSKY. Although several of the ordinary staining solutions were tried, none seemed to give as good and clear pictures as the malachite-green and gentian-violet method. The salts, which are generally placed on the slide with the bacterial preparations, especially when solutions are the origin of the material studied, are not stained by this method. The technic is as follows: The coverglass preparation, flame fixed, is mordanted for 1 minute in the cold with a 0.25 per cent solution of malachite-green in distilled water, washed with cold water, and stained cold with a 0.25 per cent water solution of gentian-violet for 1 more minute. Washing is then done rapidly with water previously heated to 50–60° C. This washing takes out any coloration of the salts which might cloud the microscopic field. Preparations are thus obtained which stain the jelly of the megalococci a deep purple and the small cocci of the β type a purple-black color. Treatment with acid is not necessary to dissolve the salt formations. In the fresh unstained state the cells are not easily visible, and a search for them often proves unsuccessful. The color differentiation mentioned, obtained in Meissner solution, constitutes what seems to be the best and most reliable one for a study of the organisms in hanging drop preparations.

Temperature relations

The thermal death point of the organism studied was found to lie between 50 and 55° C., when the vitality of the organism, after heating 5.5 minutes at the required temperature, was tested at rest in OMELIANSKI'S solution containing basic magnesium carbonate. An additional study of the resistance of the organism to heat was also made. One cc. portions of a strong nitrifying culture were placed in sterile vials, heated at given temperature for given lengths of time, and then quickly cooled in stone cold water, the depth of the solution layer being 4–5 mm. over a surface of ± 2.8 cm^2. Heating was done in ovens, and tests for

the vitality of the cultures were made by inoculating all the heated material in large test-tubes containing 25 gm. of sterile coarse ignited soil and $MgCO_3$ kept in a slanting position by 10 cc. of sterile OMELIANSKI solution. Duplicates were run for each treatment. When the cultures were tested for the formation of nitrite after 12 days of incubation at 30° C., the results given in table III were obtained.

Although the duration of incubation was not very long, the nature of the medium was such as to allow complete nitrification in all cases where full inoculum was used. The fact that a heating of 40 minutes at 50° C., a heating of 10 minutes at 55° C.,

TABLE III*

Temperature of heating	Time of heating in minutes					
	2	5	10	20	40	60
45° C.	+	+	+	+	+	+
50° C.	+	+	+	+	o	
55° C.	+	+	?			
62–65° C.	+	o				

*The + indicates a strong nitrite formation, ? a questionable nitrite formation, and o no nitrite formation.

and a heating of 5 minutes at 62–65° C. gave questionable or negative nitrification, while all other cultures gave complete nitrification, is very significant.

BOULLANGER and MASSOL (3) found the thermal death point of the organism of nitrosofermentation isolated in their work to lie between 45° and 50° C. when the heating continued for 5 minutes. It is seen, therefore, that the organism isolated from Wooster soils resists higher temperatures and longer periods of heating than the one which constituted the object of their studies. The difference in apparatus used might lead to slight variations in the T.D.P. determinations.

The incubation of all the cultures of nitrite-formers cultivated in this laboratory has been done at 28–30° C. At this temperature cultures were obtained which nitrified as much as 8.04 mg. of ammoniacal nitrogen in 26 days of incubation at rest.

Discussion

The results of this study on the morphology of the organisms of nitrosofermentation, active in the North American soils, are not easily reconciled with the results obtained 28 years ago by JORDAN and RICHARDS. The discrepancy between the results is undoubtedly to be ascribed to two reasons: (1) incomplete description of the organisms isolated from sewage in Massachusetts, and (2) the probable presence in those cultures of organisms capable of transforming nitrites to nitrates. The possibility of a mixed culture was admitted by JORDAN and RICHARDS on the basis of the absence of nitrite formation during nitrification.

The resemblance of the megalococcus isolated by WINOGRADSKY from the South American soils to the megalococcus for the North American soils is quite striking. Excepting the slight difference in size existing between the two forms, all other characters are common to both. The variation in the life cycle of the two organisms is probably only apparent, since the true cocci, which have been named β by the author, might have escaped WINOGRADSKY's attention. It is to be regretted that the Russian investigator was not able to study the nitroso-organisms from the New World as thoroughly as he did those from the Old World, and that he was obliged to publish only an abridged description of the former types. In the present work an attempt was made at the completion of his work, and results have been reached which corroborate the postulations to be made from his findings, in such a way filling a gap in our knowledge of the distribution of the nitrite-forming organisms. That the organism isolated in Wooster can be classed as a species of the genus *Nitrosococcus* seems to be justified by these findings. The comparative study of the species of the genus *Nitrosococcus* will have to be deferred to a time when a careful study will be possible of the organisms of nitrosofermentation in South America and Australia.

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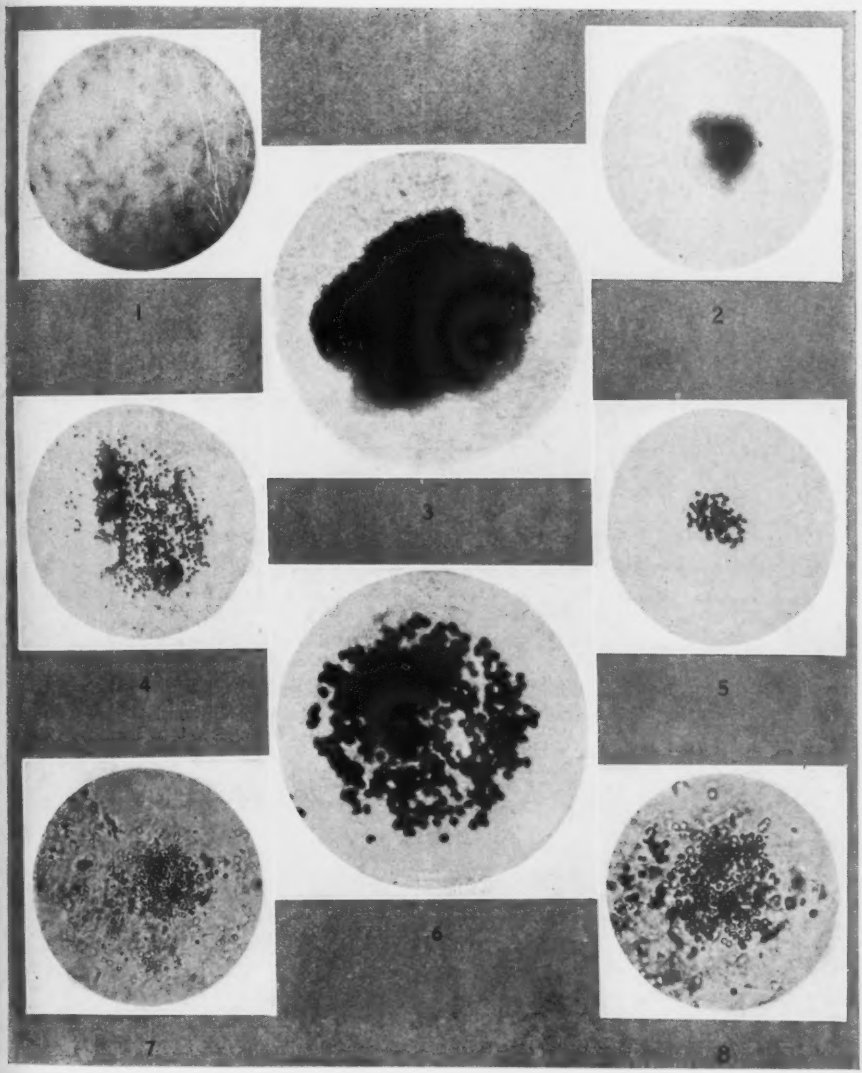

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EXPLANATION OF PLATE XIV

The photomicrographs were made with the kind assistance of Mr. VICTOR DYE, photographer of the Station.

FIG. 1.—Portion of silica jelly plate, showing colonies of *Nitrosococcus* after several additions of ammonium sulphate; solubilization of magnesium carbonate in vicinity of colonies very evident; ×1.5.

FIG. 2.—Colony of *Nitrosococcus* on silica jelly plate, showing loosely granular structure, as seen against a source of light; ×77.

FIG. 3.—Another colony on silica jelly; ×175.

FIG. 4.—*Nitrosococcus* from culture undergoing intensive nitrification, showing lack of zooglea formation; stained by malachite-green–gentian-violet method of WINOGRADSKY; ×820.

FIG. 5.—*Nitrosococcus* from culture undergoing intensive nitrification, showing small β forms imbedded in thick gelatinous membrane; cocci and diplococci; stained by malachite-green–gentian-violet method of WINOGRADSKY; ×820.

FIG. 6.—*Nitrosococcus* from culture undergoing intensive nitrification, showing typical megalococci; in some cases the small forms are seen appearing in thick gelatinous membrane, stained by malachite-green–gentian-violet method of WINOGRADSKY; ×1600.

FIG. 7.—*Nitrosococcus* in hanging drop preparation, stained with Meissner's solution; ×740.

FIG. 8.—*Nitrosococcus*, same as no. 7; ×1200.

POLYXYLIC STEM OF CYCAS MEDIA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 252

WARD L. MILLER

(WITH ELEVEN FIGURES)

The question which lends particular interest to the polyxylic situation in 4 of the cycad genera (*Cycas*, *Macrozamia*, *Encephalartos*, and *Bowenia*) is whether or not the separate, concentric, vascular cylinders all originate with the differentiation of procambium strands in the plerome cylinder, and whether or not true protoxylem and protophloem are formed in every or in any instance. If protoxylem and protophloem are formed, are they or are they not orthodox in their detailed structures, and what is their condition in the older parts of the stem?

It is the purpose of this investigation to discover the exact origin and behavior of the different cambiums which develop the separate vascular cylinders, and to formulate some definite conclusions regarding the vascular elements which will leave the matter of this unusual method of secondary growth more clearly understood.

Historical

Although research among the cycads has been comparatively limited by lack of suitable material for study, several accounts have been published which deal more or less directly with the present problem. During an investigation of *Cycas siamensis* in 1885, CONSTANTIN and MOROT[1] concluded that the cambium of each supernumerary zone, laid down outside the first or normal cylinder, originated in the pericycle of the cylinder next inside.

In 1896 WORDSELL[2] published an account of the polyxylic stem of *Macrozamia*. In this particular genus he found the corti-

[1] CONSTANTIN, J., and MOROT, L., Sur l'origine des faisceaux libéro-ligneux supernuméraires dans la tige des Cycadées. Bull. Soc. Bot. France 32:173. 1885.

[2] WORDSELL, W. C., Anatomy of stem of *Macrozamia* compared with that of other genera of Cycadeae. Ann. Botany 10:601–620. 1896.

cal cylinders diminishing in the thickness of their wood and phloem as they neared the tip of the stem, until finally they disappeared entirely, the outermost disappearing first and the innermost last. Protoxylem, at least of the spiral kind, he found to be entirely obliterated in the normal cylinder, although it seems to have been of frequent occurrence in the leaf traces, where the crushing pressure of thickening cells was less effective. He mentions no protoxylem in connection with the supernumerary cylinders, either as to its presence or absence, nor in connection with leaf traces coming from these cylinders.

SCOTT'S[3] work in 1897 led him to the conclusion that the polyxylic habit was a derivation from the habit of ancient stems among the Cycadofilicales which developed layers of concentric bundles, for example, *Medullosa*.

WORDSELL[4] again in 1900 published an account of the seedling stem structure in *Bowenia*. There he found beginnings of a supernumerary vascular cylinder outside the normal one. Hints of concentric bundles, which he found in *Bowenia* and earlier in *Macrozamia*, led him to agree with SCOTT in the idea of the phylogenetic origin of supernumerary cylinders.

COULTER and CHAMBERLAIN[5] published in 1910 a summary of previous investigation pertaining to the vascular anatomy of cycad stems, and in addition gave a short description of the gross topography of the polyxylic habit.

JEFFREY'S[6] work, published in 1917, is the most recent account of this cycad peculiarity. To him also it is apparent that supernumerary cylinders arise in the pericycle. He objects, however, to SCOTT'S conclusions in regard to the phylogenetic origin of these vascular cylinders; he believes rather that they are a result of an ancient climbing habit of the stem. Such situations, he says, are frequent in numerous climbing stems of the present time, stems of both gymnosperms and dicotyledonous angiosperms.

[3] SCOTT, D. H., The anatomical characters presented by the peduncles of Cycadaceae. Ann. Botany 11:399–419. 1897.

[4] WORDSELL, W. C., The anatomical structure of *Bowenia spectabilis*. Ann. Botany 14:159–160. 1900.

[5] COULTER, J. M., and CHAMBERLAIN, C. J., Morphology of gymnosperms. 1910.

[6] JEFFREY, E. C., The anatomy of woody plants. 1917.

The foregoing brief account of previous research, touching upon the problem at hand, gives a foundation upon which to work and from which to develop further lines of investigation.

Material and methods

Material used in the study of the problem was collected by Dr. CHAMBERLAIN near Rockhampton in Queensland, Australia. I take this occasion to express my appreciation of his generosity in giving up material from his own private collection for my study, and of his helpful suggestions during the investigation. The plant collected by CHAMBERLAIN was about 3 m. in height, as it occurred in nature, and bore at its tip a cluster of megasporophylls surrounded by a crown of foliage leaves. Two pieces were taken from the stem, one at the apex and one near the base. The former piece was the entire tip, including the upper 6 or 8 inches of the axis, together with foliage leaves and megasporophylls; the latter piece was a cross-section of the stem at a height of less than a foot above the soil, and was cut with a thickness of about 3 inches. Both pieces were put into formalin, where they have remained since the time of their collection in November 1911.

Pieces of the stem were thoroughly washed in water and then allowed to stand in 50 per cent hydrofluoric acid for a period of 4 weeks. Following this treatment, methods were employed which were based upon the fundamentals of technic as published by CHAMBERLAIN[7] in 1916. Such variations in these principles as were used grew out of the kindly suggestions of Miss LANGDON of this laboratory. To her my thanks are given for her valued assistance.

Investigation

GROSS TOPOGRAPHY

As would be expected, the pith of this specimen is relatively large. Its diameter at the stem base measures 5.3 cm., whereas the diameter of the entire stem at the base is only 20 cm. At the tip, where the gross diameter is 17.8 cm., the pith has a diam-

[7] CHAMBERLAIN, C. J., Methods of plant histology. 1916.

eter of 5.8 cm. There is practically no tapering to the columnar trunk excepting at the very apex, while the pith actually increases in diameter as it nears the apex, until it finally merges into the plerome cylinder (fig. 1).

At the base of the stem there are 3 separate and distinct vascular cylinders, the normal one nearest the pith and the 2 cortical ones developed concentrically about the normal. In previous accounts the first cortical cylinder has been reported to have a development of xylem and phloem equal to that of the normal cylinder, while the second and succeeding cortical cylinders diminish successively in that development toward the periphery of the stem. I find in this stem, however, that, near the base, the first cortical cylinder has a greater radial extent of xylem and phloem than has the normal one, while the second is about the equal of the normal, thus beginning the successive decrease of xylem and phloem development which would likely be continued further if other vascular cylinders were present (fig. 2). In each cylinder the xylem elements are of greater radial extent than phloem elements, the former occupying approximately three-fifths of the radial extent of the entire cylinder.

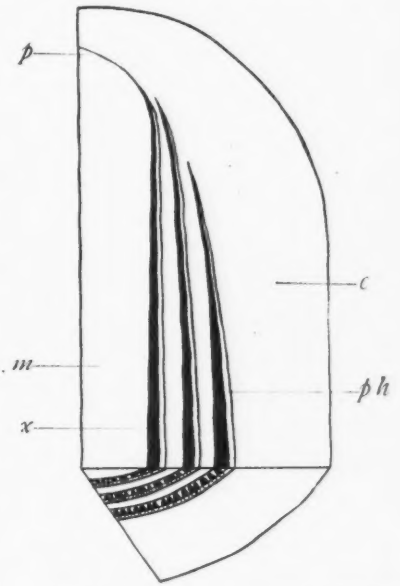


FIG. 1.—*Cycas media:* showing radial and transverse aspects of polyxylic stem near tip; *m*, pith; *p*, plerôme; *x*, xylem; *ph*, phloem; *c*, cortex.

At the stem apex only 2 vascular cylinders are evident (fig. 3). Here the normal cylinder is seen to have xylem and phloem of slightly less radial extent than it has near the stem base, while

the first cortical cylinder has decreased so much in its dimensions that it is barely visible to the unaided eye. Furthermore, the latter occurs, not as a continuous cylinder, but rather as a cortical layer of separate, broad, and short bundles which are distinctly collateral. The outermost cortical cylinder entirely disappeared before reaching the height at which the section was taken. This

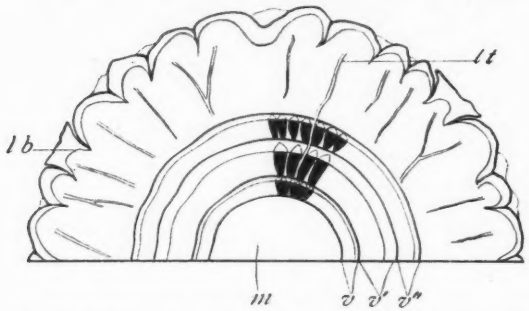


FIG. 2.—*Cycas media:* showing gross topography of transverse section of stem near base; *v*, *v'*, *v''*, 3 distinct vascular cylinders; *m*, pith; *lt*, leaf traces; *lb*, leaf bases.

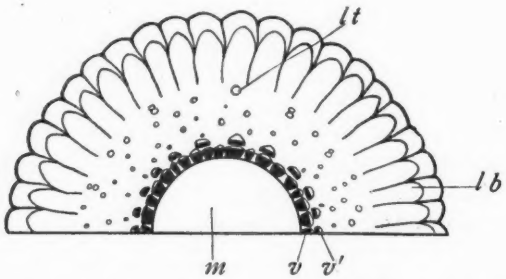


FIG. 3.— *Cycas media:* showing gross topography of transverse section of stem near tip; *v*, *v'*, 2 vascular cylinders; *m*, pith; *lt*, leaf traces; *lb*, leaf bases.

quite agrees with WORDSELL'S (*loc. cit.*) account of a situation exactly similar in *Macrozamia*. Fig. 1 represents the polyxylic structure diagrammatically, as it might be seen in radial section in the apical region of the stem. Differentiation which results in cortical cambium begins farther from the stem apex in each succeeding cylinder, being farthest in the outermost cylinder.

The cortex, true to cycadean character, is relatively large, as well as the pith. At the stem base the cortex measures 2.9 cm. between the outermost cortical cylinder and the leaf base, and at the tip 2 cm. A great many leaf traces traverse the cortex. At the base of the stem these traces are seen in longitudinal section (fig. 2), excepting at those places where they are just leaving the vascular cylinder. At the tip, however, leaf traces are invariably seen in transverse section (fig. 3), and they are characteristically double where they are about to enter a leaf base. Traces may leave any or all of the vascular cylinders, those from the inner ones passing to the cortex through the medullary rays of one or more outer cylinders.

DETAILED STRUCTURE

Normal cylinder.—Vascular bundles of the normal cylinder are long and narrow in transverse section (fig. 4), rarely becoming more than 3 or 4 cells in tangential thickness. Bundles taper to a rather sharp point toward the pith, and there is located the definite endarch protoxylem. Wordsell had difficulty in locating protoxylem in the stem of *Macrozamia* which he studied, for it had been obliterated by the crushing caused by thickening wood cells. In the specimen which I studied the protoxylem is still intact in the majority of cases, and is easily distinguished (fig. 4). Fig. 5 represents protoxylem of the normal cylinder, enlarged enough to show its detailed character. The cell walls are less thickened than those of the primary xylem above, and there are certainly no pits present, as there would be if the xylem were of secondary origin. In this particular instance pits are absent from the primary xylem also. This is an unusual condition, since, as in fig. 6, primary xylem of the normal cylinder is practically always scalariform. Fig. 6 shows the radial aspect of the normal cylinder in its centripetal region. Here protoxylem elements are unquestionably spiral in character, while the succeeding primary xylem is scalariform. It should be said here that spiral tracheids are of comparatively rare occurrence even in the normal cylinder; at least they are rare in stretches large enough to be correctly interpreted. The usual form of protoxylem is scalariform rather

than spiral. Since neither transverse nor radial preparations show crushed masses of cellular material at the centripetal ends of bundles, there can be no doubt that the xylem elements which can be seen to terminate the bundles are truly protoxylem, whether they are spiral or scalariform.[8]

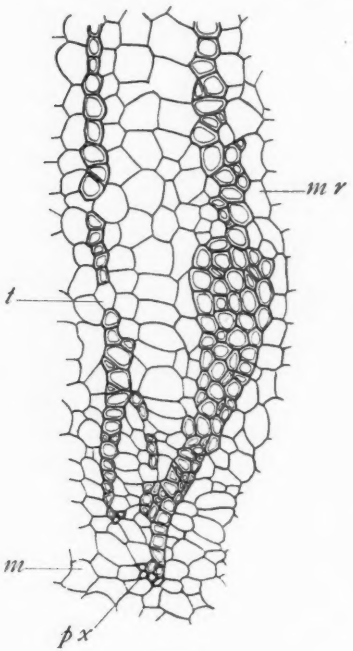


FIG. 4

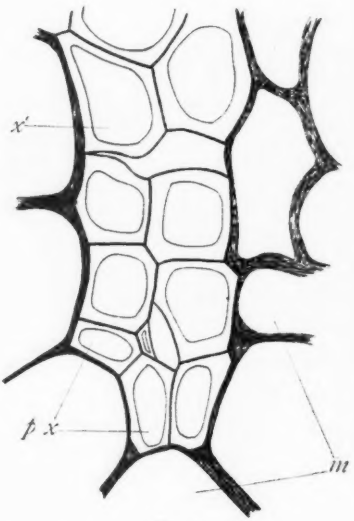


FIG. 5

FIGS. 4, 5.—*Cycas media:* fig. 4, transverse section of stem, showing only centripetal end of bundle of innermost cylinder; *m*, pith; *mr*, pith ray; *px*, distinct protoxylem; *t*, unthickened xylem elements; ×400; fig. 5, transverse section of stem, showing centripetal end of bundle of innermost cylinder highly magnified; *m*, pith; *px*, protoxylem; *x'*, primary xylem; pits apparent in none of these cells; ×850.

As in WORDSELL'S account, spiral tracheids here can be followed more easily in leaf traces off the normal cylinder than they can in the cylinder itself. The reason for this is not that these elements have been destroyed in the cylinder proper, but that

[8] CHAMBERLAIN, C. J., The adult cycad trunk. BOT. GAZ. 52:97. 1911.

they meander back and forth tangentially, so that only short patches can be caught here and there in a single radial section. The meandering habit is not so pronounced in the traces, and consequently longer stretches of primitive xylem elements can be seen and identified as such.

Secondary xylem of the normal cylinder is composed of tracheids which are characteristically pitted, the pits being confined largely to the radial walls, as described by both CHAMBERLAIN and JEFFREY.

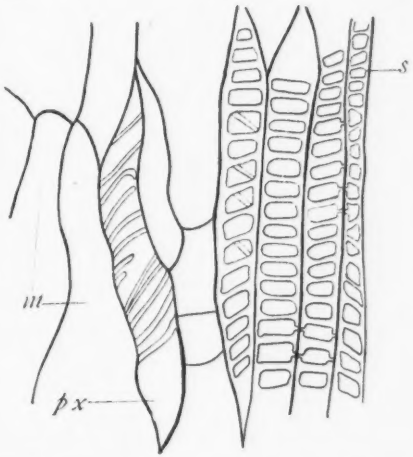


FIG. 6.—*Cycas media:* radial section of stem, showing centripetal end of bundle of innermost cylinder; *m*, pith; *px*, protoxylem distinctly spiral; *s*, scalariform tracheids of primary xylem, left one also having spiral thickenings; ×400.

The phloem situation of the normal cylinder adds emphasis to the fact of the latter's procambium origin, for protophloem is as distinct here as it is in any of the typical monoxylic cycad stems. Fig. 7 illustrates the upper phloem region of this cylinder, showing the crushed cellular substance which once was organized protophloem. This dark crushed mass has the appearance of a thick irregular ring in transverse section, entirely surrounding the normal cylinder and immediately inside the centripetal limits of the first cortical cylinder (fig. 8). The ring of course is interrupted here and there by medullary rays, but in many cases it extends unbroken across them, being squeezed in between the cells of the pith or cortical medulla. From this protophloem center primary and secondary phloem extend, fanlike, outward and downward in typical fashion. The rather startling character of the secondary phloem is its large number of suberized bast fibers compared to the number of sieve tubes. The former far

outnumber the latter, which occur here and there in short tangential rows between the bast.

FIRST CORTICAL CYLINDER.—The most intensive study of the cortical cylinder was made from preparations of the innermost one near the apex of the stem (fig. 3). Here details could be observed where the cylinder was in an early stage of development, and where its character could best be determined.

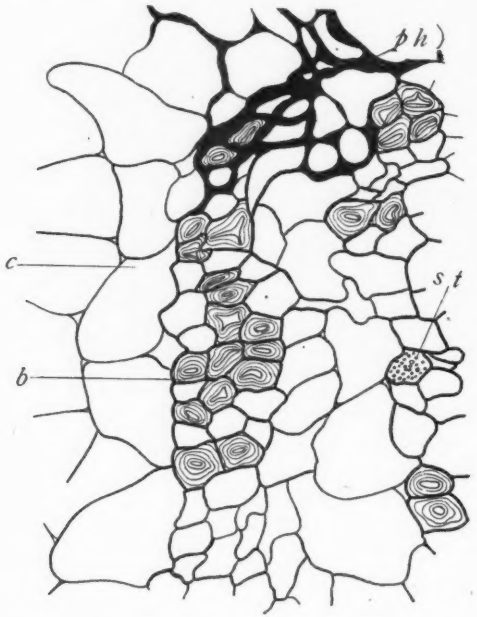


FIG. 7.—*Cycas media*: transverse section of stem, showing region of protophloem of innermost cylinder; *ph*, protophloem; *b*, suberized bast fibers of secondary phloem; *st*, sieve tube; *c*, cells of cortex; ×235.

Fig. 8 shows a transverse section of the entire cylinder, together with regions bordering it on both inner and outer boundaries. Apparently no protoxylem is present in these bundles. Cells at the centripetal limit of a bundle are not different from those nearer the cambium; there is little or no difference in size, shape, and thickness, in alignment, or in the character of cell

walls. Fig. 9 shows characteristics of the xylem in that region of the cylinder where protoxylem would be expected if there were any. All cells are uniformly thickened and, without exception, equipped with bordered pits, which is always a mark of secondary origin. In fig. 10 the same region is seen in radial section. Here the xylem element nearest the stem center, and even bordering on protophloem of the normal cylinder, is pitted. This one drawing illustrates tracheids of the first cortical cylinder which are as nearly scalariform as could be found; they are as rare as spiral tracheids are in the normal cylinder. By far the greater number of xylem elements in this centripetal region of the cylinder are pitted in exactly the same fashion as ordinary secondary tracheids of the normal cylinder, and they must in turn be considered as of secondary origin.

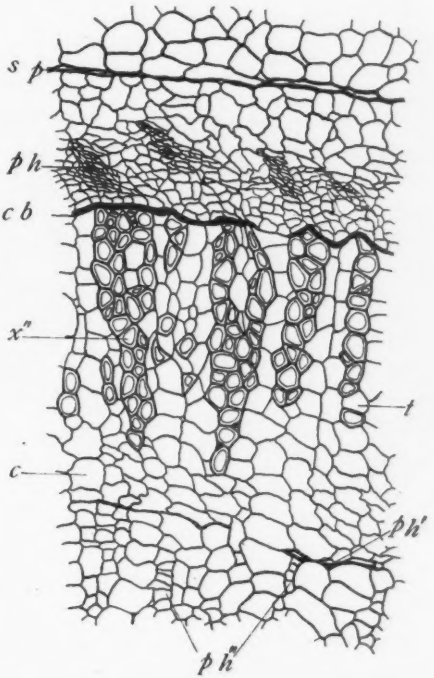


FIG. 8.—*Cycas media:* transverse section of stem, showing entire second cylinder as it appears near tip of stem; *ph'*, protophloem of first cylinder crushed; *ph''*, secondary phloem of first cylinder; *c*, cortical cells; *x''*, secondary xylem of second cylinder; *t*, unthickened xylem cells; *cb*, cambium; *ph*, secondary phloem of second cylinder; *sp*, split in cortex caused by expansion lower down of third cylinder; ×85.

In fig. 8 it will be seen that the region between the normal cylinder and the first cortical one is composed of purely cortical cells. Also the region between the first cortical cylinder and the split in the cortex, which marks the place where the second

cortical cylinder will appear, is purely cortical. No differentiation is evident between stelar pericycle and cortex; there is even no endodermis, and therefore there is no ground here for believing that the supernumerary cylinders originate in the pericycle. In view of Sister HELEN ANGELA'S[9] work with *Ceratozamia*, in which she found unquestionable cambiums at any place in the cortex from the stele to the periphery, it would be possible for the supernumerary cylinders of *Cycas* to originate in the cortex. In view of the evidence of fig. 8 it would also seem probable that the cylinders are truly cortical and not stelar.

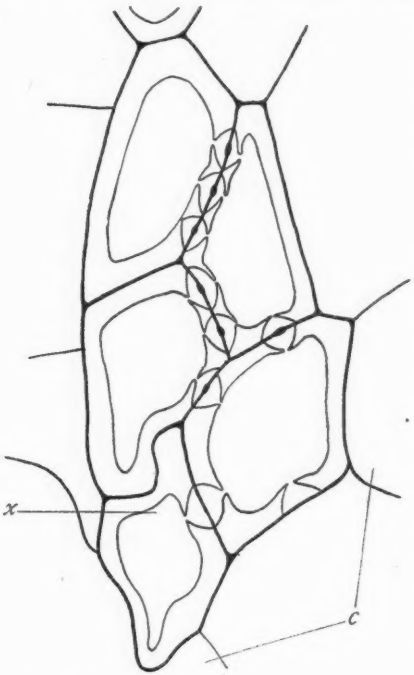


FIG. 9.—*Cycas media:* transverse section of stem, showing centripetal end of second cylinder; *c*, cortical cells; *x*, distinctly pitted xylem cells at tip of bundle; ×850.

There is no evidence of protophloem in connection with the cortical cylinder. A transverse section (fig. 11), which is thoroughly representative of the state of affairs, shows that practically all cells of the phloem are suberized bast fibers. This, together with the very apparent alignment of the fibers, is convincing proof that no protophloem is present.

Sections of the first cortical cylinder near the stem base reveal conditions almost identical with those of the normal cylinder, excepting that in the former both protoxylem and protophloem

[9] DORETY, HELEN A., The extrafascicular cambium of *Ceratozamia*. BOT. GAZ. 47:150–152. *pl.* 7. 1909.

are absent. Bundles of the former resemble those of the latter in shape, the secondary alignment of the former being disturbed by unequal growth and pressure, and bundles of both are of about equal size, those of the cortical cylinder being a little longer radially. Both cylinders give off leaf traces which differ in respect to the presence or absence of protoxylem and protophloem.

OTHER CORTICAL CYLINDERS.—There is little reason for believing that the second and succeeding cortical cylinders would have

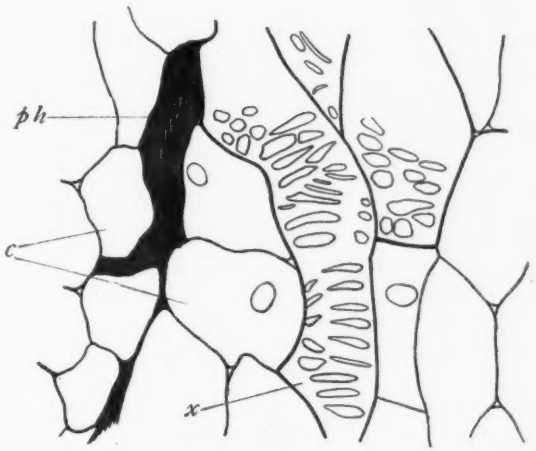


FIG. 10.—*Cycas media:* radial section of stem, showing centripetal end of second cylinder; *c*, cortical cells; *ph*, crushed protophloem of first cylinder; *x*, innermost xylem elements of cylinder, showing distinct pits, some having fused; ×400.

a mode of origin and development different from that of the first; consequently but little time was devoted to the study of the second cortical cylinder. Preparations from the stem base only were examined, and, as was expected, these showed conditions in the mature part of the stem identical with those of the first cortical cylinder in the same region. Further discussion, therefore, would be but a repetition of what has been recorded thus far.

In concluding the matter of cortical cylinders it may be well to mention the relationship of their number to the age of the plant. Certainly they do not occupy the position of growth rings, nor

are they laid down at regular intervals of time. The plant which was studied was more than a century old and yet had but 3 vascular cylinders. Doubtless the cortical cylinders are related to certain activities of the plant alternating with long periods of rest which may vary greatly in point of duration.

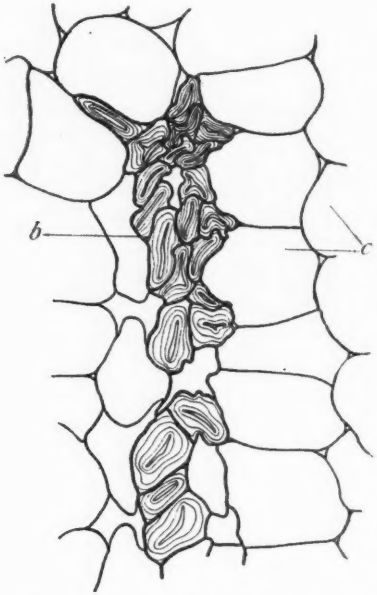


FIG. 11.—*Cycas media:* transverse section of stem, showing tip of phloem belonging to second cylinder; *c*, cortical cells; *b*, suberized bast fibers; ×235.

Summary and conclusions

1. The paper deals with the adult stem of *Cycas media*, particular attention being paid to the xylem and phloem details of the normal and first cortical cylinders.

2. Not all the vascular cylinders are of equal longitudinal extent. Only the normal one begins its differentiation as high up as the meristem, the others beginning their differentiation successively lower, and each one in the cortex outside the next inner cylinder. The normal cylinder, therefore, is the only one which would be expected to originate with a procambium, and the only one which could develop protoxylem and protophloem.

3. Following up these expectations, both protoxylem and protophloem were found to have been developed during the early activities of the normal cylinder. Protoxylem elements are usually scalariform, although hints of spiral tracheids are more or less frequent. Primary xylem is scalariform and secondary xylem is characteristically pitted.

4. Neither protoxylem nor protophloem was found in the first cortical cylinder. Practically all of the xylem elements are pitted, but scalariform tracheids are occasional.

5. The secondary phloem of both cylinders is characterized by the great number of suberized bast fibers compared to the number of sieve tubes.

6. All cortical cylinders are similar in respect to their origin and development and are probably related in their appearance to the alternating periods of rest and activity of the plant.

7. Unfortunately material was unavailable which would have shown the beginning of differentiation of a cortical cambium. Such a piece taken from the stem apex would have been far enough up to destroy material needed for further research.

UNIVERSITY OF CHICAGO

A PARASITE OF THE TREE FERN (CYATHEA)

F. L. STEVENS AND NORA DALBEY

(WITH PLATES XV, XVI)

Cyathea arborea (L.) J. E. Smith, one of the most beautiful of the Porto Rican tree ferns, is usually heavily infected by black fungous growths. Two collections of this fungus were made, one at Maricao, July 19, 1915, the other on El Alto de la Bandera, July 14, 1915.

On the older leaves the fungus is so abundant that the smallest frond segments, which measure about 3×7 mm., bear 25 or more of the black spots, and no segment is free of the fungus. On comparatively young fronds infections are less numerous, but even on such there are many fungous spots. A general idea of the appearance of the disease may be gained from figs. 1 and 2. The spots are often so abundant as to occupy considerably more than half of the leaf area. The individual spots are irregular in outline, and slightly elongated in a direction parallel with the veins of the host. The center of the spot is occupied by a conidiiferous structure, oblong, flattish, and dimidiate. This opens by an irregular crack, and in old pycnidia the whole top falls away (fig. 3). The cleavage lines seem to be determined by irregular rows of large cells. Immediately surrounding the pycnidium is seen a subiculum composed of close hyphae which appear to radiate much after the manner of the Microthyriaceae (fig. 4). Close focusing shows that this layer, instead of being superficial, is within the epidermal cells. Surrounding this epidermal subiculum is an area in which mesophyll cells alone are diseased. The diseased cells are dark brown and are quite filled with the coarse dark mycelium, while the adjacent cells are normal. In the cases of very young diseased spots, consisting of only a few cells, the infection is entirely in the mesophyll (fig. 19). It is only later that the central epidermal cells of a spot become invaded.

In microtome section these facts are verified: the mesophyll cells are seen to be invaded first, later the epidermal cells. Then the

fungus emerges and lays down a membrane one cell thick, of dark, thick-walled, closely woven hyphae. Under this arise in a close group numerous erect cells which in section appear like a palisade formation (fig. 6). These cells elongate; the covering layer becomes arched and eventually ruptures. The palisade-like cells are really conidiophores and bear the large, dark, 1-celled spores (fig. 8). The pycnidia are often sterile, the conidiophores then becoming greatly overgrown and distorted. The conidia germinate upon the surface of the leaf, producing at once an appressorium (fig. 9), which doubtless lends itself to the leaf invasion. This conidial structure is clearly of the Leptostromataceae-Phaeosporae, but does not fit well any of the form genera there given.

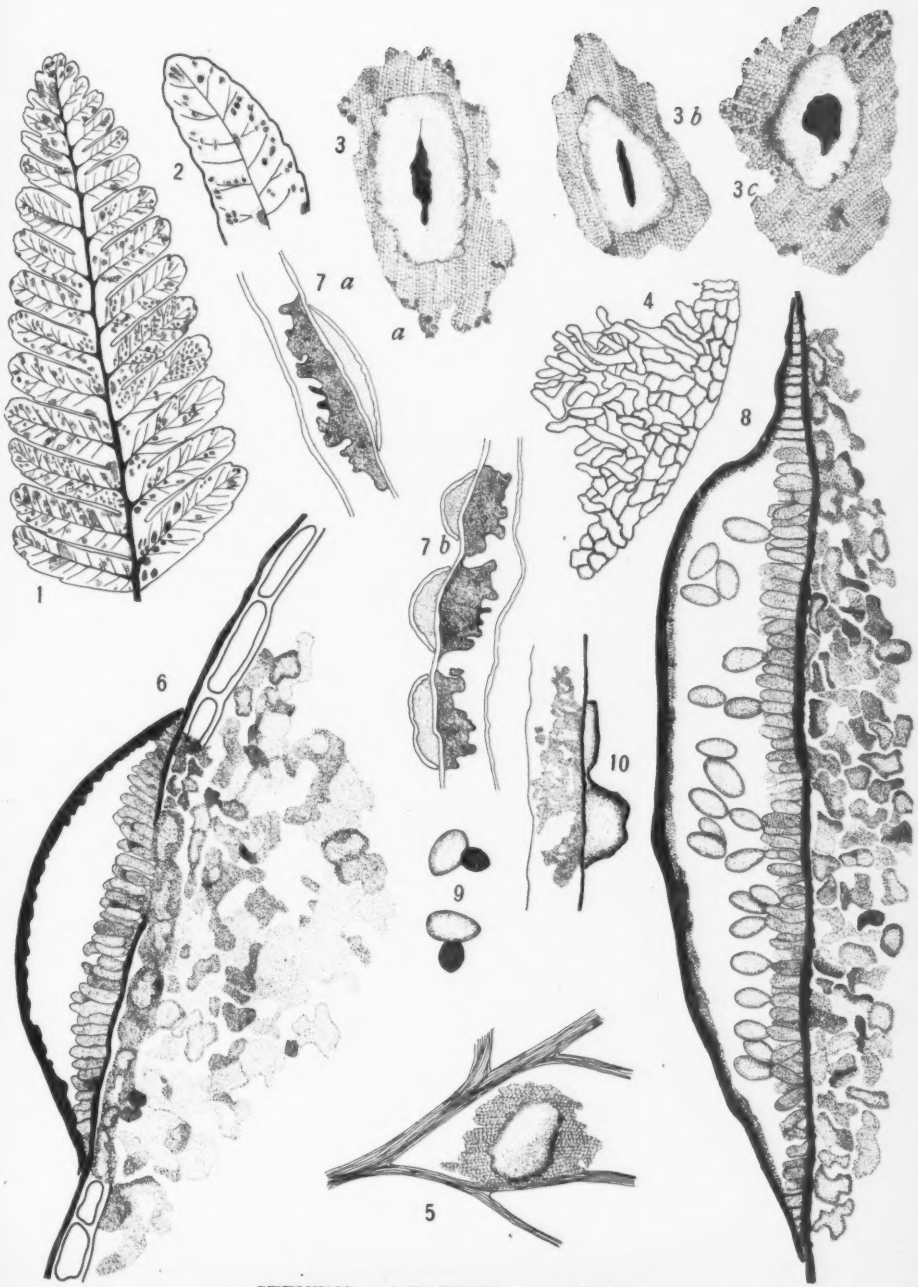
The infected spots give rise also to perithecia, although these are much less abundant. The perithecia at maturity are high and rounded (figs. 11*a*, 11*b*, 14, 15). The perithecial wall is composed of several layers of dark cells, compressed to a pseudoparenchyma (fig. 12). The perithecia are uniform in shape, with a domed top; that they arise from the same mycelium which produces the pycnidia is clear (fig. 10). The young perithecia are indistinguishable from pycnidia, and indeed it appears that a pycnidium which is not yet sporiferous can develop into a perithecium. The first indication of differentiation is that in the perithecia a bed of closely packed hyaline mycelium develops between the cuticle and the covering. Soon the top begins to arch and to lay on internally added layers in thickness. The pycnidium covering is only one cell thick, the perithecium covering always several cells thick. At maturity the perithecial wall is lined by a layer several strands thick of felted hyaline mycelial threads. The asci, which are not numerous, arise basally, various ages side by side, and interspersed with numerous long mycelial threads (fig. 14) which may be regarded as paraphyses, although they are far from typical paraphyses in appearance. The basal structure of both the pycnidia and the perithecia consists of a dense mat of mycelium laid down in the epidermal cells. This structure is difficult to represent because in the growth process the epidermal cells are largely obliterated. The facts, however, are hinted at in figs. 6, 12, and 15. It is this epidermal subiculum which gives the radiating effect shown in fig. 18.

The questions of morphology and parasitism of this fungus are of especial interest. The morphological characters to be emphasized are the internal intracellular mycelium, the external fungous layer which becomes the cover of a dimidiate pycnidium, the dome-shaped, flat-bottomed perithecium with a wall several cells thick and without ostiole. The habit of the mycelium of completely filling certain cells or irregular groups of cells while intervening and adjacent cells are entirely free of mycelium is striking. The whole picture gives a group of characters difficult to place satisfactorily. The mycelial characters are Microthyriaceous, the absence of ostiole Perisporiaceous, and it might be possible to regard the perithecial cavity as being in a stroma and thus incline toward the Dothidiaceae. It is also possible, when the top is fallen out of the perithecium, to regard it as Phacidiaceous, and it is here that we would place it, although the mode of formation and of opening of the perithecium are not fully characteristic of that family. The genus *Rhagadolobium*, described on a tropical fern (HENNING and LINDAU in Engler's Jahrb. **23**:288. 1896), presents certain similarities in the structure of the stroma, although it differs essentially in many ways, particularly in having the mycelium intracellular rather than intercellular, and in having 1-celled spores. In the Dothidiales the fungus resembles *Rhipidocarpon* Th. and Syd. in structure of the perithecium as seen in section, but the perithecium is not radial. In fact, it presents essential differences from all of the families of the Dothidiales as set up by THEISSEN and SYDOW. The fungus clearly shows differences from established genera sufficient to render its admission to any of them impossible. We therefore propose for it the new genus:

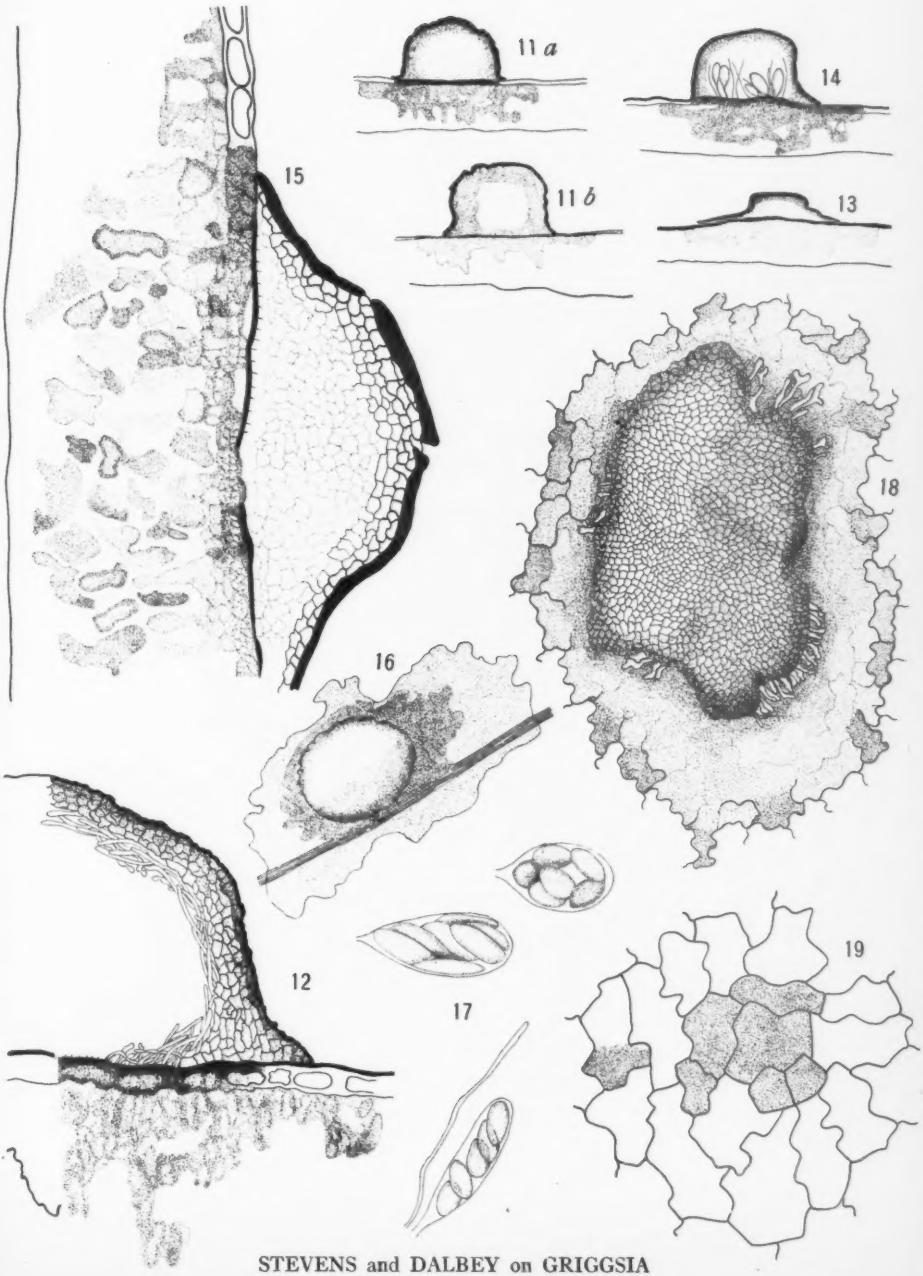
Griggsia, gen. nov.

Perithecia solitary, dimidiate, without ostiole, opening by irregular cleavage of the top, arising from a thin superficial and epidermal stroma, vegetative mycelium internal. Perithecial wall several cells thick. Asci basal, 8-spored. Spores oval, hyaline, 1-celled. Paraphyses hyaline, long, filamentous. Conidia in dimidiate pycnidia. Type species *Griggsia cyathea*. Named in honor of ROBT. F. GRIGGS.

Griggsia cyathea, sp. nov.—Perithecium dome-shaped, 200–300 μ in diameter, 150–160 μ high; wall about 24 μ thick on sides



STEVENS and DALBEY on GRIGGSIA



STEVENS and DALBEY on GRIGGSIA

and top. Asci 51×17–24 μ, ovate. Spores 10×17 μ, oval, hyaline, 1-celled.

Conidial stage: Pycnidia dimidiate, opening by a ragged cleft, amphigenous but more frequently epiphyllous, circular, 200–315 μ in diameter, 10–30 μ high, black, dimidiate, closely reticulate, reticulations about 7 μ in diameter, occupying the approximate center of a diseased spot. Spots irregular in outline, 1–3 mm. in diameter, very numerous, spores 1-celled, oval or pyriform, dark, obtuse, 28–34×14 μ.

UNIVERSITY OF ILLINOIS
URBANA, ILL.

EXPLANATION OF PLATES XV, XVI

PLATE XV

FIG. 1.—Pinnule showing distribution of disease spots.

FIG. 2.—Frond segment with spots.

FIG. 3.—Top views of pycnidia with openings.

FIG. 4.—Detail of dermal subiculum showing radiation of fibers.

FIG. 5.—Drawing showing diseased mesophyll cells surrounding pycnidium.

FIG. 6.—Young pycnidium before spores are formed, showing covering layer and conidiophores.

FIG. 7.—Pycnidia showing shape and relation to host: shading indicates diseased cells.

FIG. 8.—Detail of pycnidium with spores.

FIG. 9.—Conidia germinating, with appressoria.

FIG. 10.—Pycnidium and perithecium produced from same mycelium: shading indicates diseased region.

PLATE XVI

FIGS. 11*a*–11*b*.—Perithecia showing typical dome shape.

FIG. 12.—Detail of perithecial wall.

FIG. 13.—Perithecium in early development with merely a bed of hyaline mycelium below the covering.

FIG. 14.—Perithecium showing asci and paraphyses; diagrammatic.

FIG. 15.—Young perithecium showing progressive thickening of cells and basal structure.

FIG. 16.—Pycnidium resting on dermal subiculum: second shaded area represents diseased mesophyll cells.

FIG. 17.—Asci and spores.

FIG. 18.—Top view of covering wall of pycnidium and of subiculum showing radiate character.

FIG. 19.—Very young infected area: only mesophyll cells diseased.

ANATOMY OF LYCOPODIUM REFLEXUM[1]

J. BEN HILL

(WITH FIVE FIGURES)

In a former paper,[2] giving in some detail the results of an investigation of the development and specialization of the steles of 6 species of *Lycopodium*, I reviewed the literature of the subject of the anatomy of *Lycopodium*. The anatomical studies have emphasized "types" of steles as characteristic of various species of *Lycopodium*, among which the radial and parallel-banded arrangements predominate. In my former paper I suggested that it was inadvisable to regard any stelar arrangement as characteristic of a species of *Lycopodium*, since almost all "types" may be found in a single species, and even in a single plant at different levels in the stem.

The plants of *L. reflexum* used in this investigation were collected by Dr. C. R. BARNES and Dr. W. J. G. LAND in the vicinity of Xalapa, Mexico, in 1908. The habitat is described as moist clay soil. The material was preserved in a formaldehyde-alcohol solution and was given to me in this condition by Dr. LAND, to whom I wish to express my thanks. The slides for the investigation were prepared from paraffin serial sections cut transversely 10–15 μ in thickness and stained in safranin–light green and in iron-alum haematoxylin-safranin, both combinations producing excellent results; the former is slightly better for differentiating protoxylem in sections of young stems, and the latter better for older tissues.

Investigation

In a study of the sections of the stem the most important matter of interest is concerned with the so-called "types" of stele to be found in *L. reflexum;* a secondary significant feature is

[1] Contributions from the Department of Botany of the Pennsylvania State College, no. 17.

[2] HILL, J. BEN, The anatomy of six epiphytic species of *Lycopodium*. BOT. GAZ. 58:61–85. *figs. 28.* 1914.

the presence of cortical roots. These originate in a manner similar to that described by Miss STOKEY[3] for *L. pithyoides*, and show a

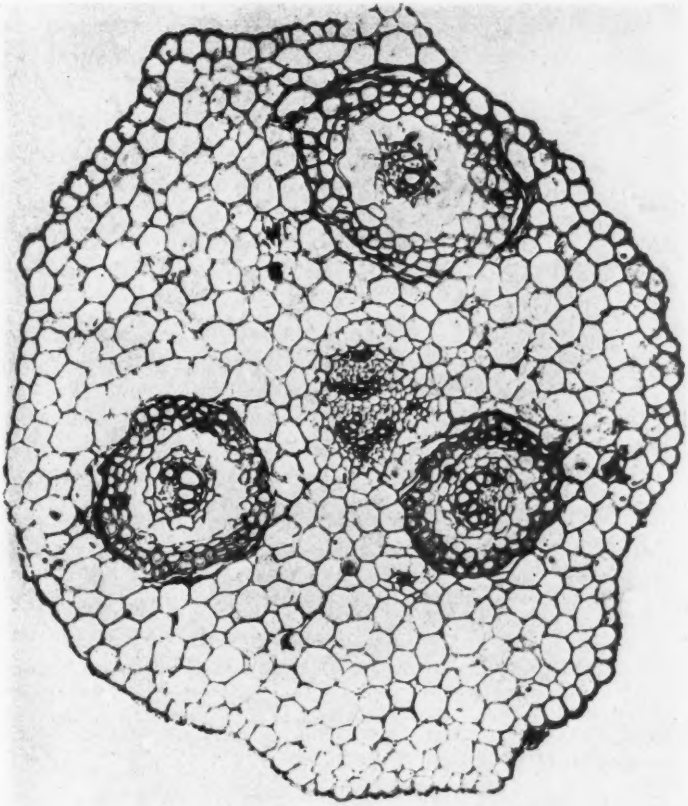


FIG. 1.—*L. reflexum:* transverse section of stem showing small stele and 3 cortical roots; in the roots phloem is surrounded by a crescent-shaped mass of xylem; root stele is surrounded by very thin-walled cells which generally are crushed and broken in sectioning; outer cortex of root composed of thick-walled cells; ×120.

development in the matter of differentiation of the stele paralleling that described[4] for the stem of *Lycopodium*, in which the xylem

[3] STOKEY, ALMA G., The roots of *Lycopodium pithyoides*. BOT. GAZ. 44:57–63. *pls. 5, 6.* 1907.

[4] HILL, J. BEN, *loc. cit.*

regions are recognizable long before lignification occurs. In young sections of the roots the metaxylem cells are recognizable early by their increased size and lack of protoplasmic content. The xylem is crescent-shaped, the protoxylem occurring at the ends and bordering the larger arc of the crescent. The mature roots, 2 or

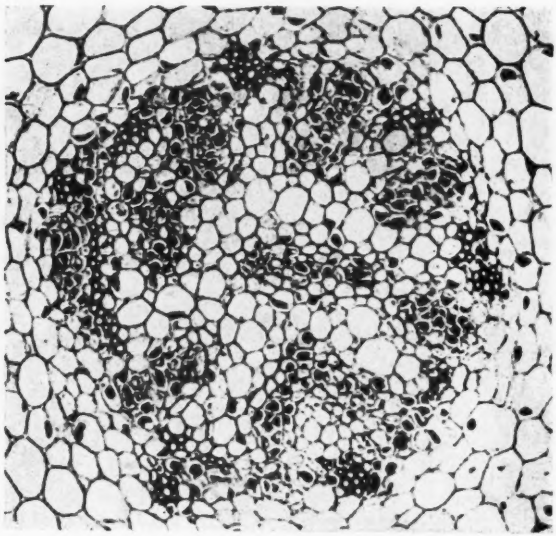


FIG. 2.—*L. reflexum:* transverse section through young stem tip showing several protoxylem points alternating with phloem in stele; phloem extends toward center of cylinder, alternating with unlignified metaxylem cells; there is a phloem island entirely surrounded by unlignified metaxylem cells; this arrangement when mature is represented in fig. 5; ×200.

3 in a stem, are typical cortical roots (fig. 1). The stem of *Lycopodium reflexum* is small, about 1 mm. or less in diameter, with a very small stele, 0.2 mm. in diameter.

In stating the results of the investigation of the steles of the stem of *L. reflexum* I shall include simply a brief description of the steles found in the stems of various ages, omitting the details of the development of the types, which were given in the former article and do not seem to vary much in different species.

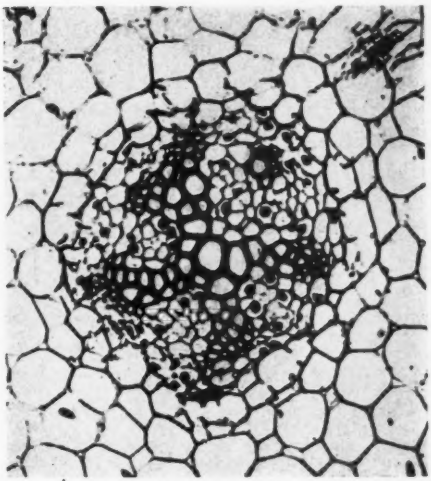


FIG. 3.—*L. reflexum:* stele showing radial arrangement of xylem with phloem located between protoxylem points and extending toward center of cylinder; ×200.

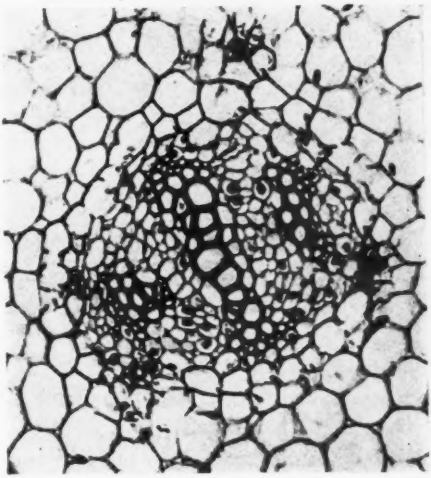


FIG. 4.—*L. reflexum:* stele showing parallel-banded arrangement of xylem with phloem occurring in bands alternating with xylem and extending across cylinder; ×200.

The number of protoxylem points in the stem stele ranges from 4 to 11, with about 7 as the most frequent number. Sections of the young stem tip show the condition characteristic of *Lycopodium*, in which at about the time of differentiation of the protoxylem points the metaxylem cells are distinguishable by their large size and lack of protoplasmic content (fig. 2). There are 3 so-called types of stele to be found in *L. reflexum:* the radial arrangement (fig. 3), the parallel-banded arrangement (fig. 4),

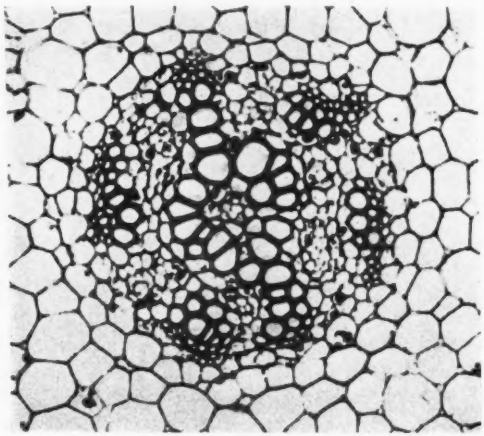


FIG. 5.—*L. reflexum:* stele showing inner cylinder of xylem surrounding strand of phloem, most frequent arrangement found in stele of *L. reflexum;* ×200.

and an arrangement consisting of an inner cylinder of xylem surrounding a strand of phloem (fig. 5). These 3 arrangements of the xylem may be found in the same stem at different levels, and are all modifications of the radial arrangement. The parallel-banded arrangement, in which alternating strands of xylem and phloem occur in parallel bands across the cylinder, seems to be correlated to some extent with the growth of roots, since this arrangement is to be found most frequently in the region where the roots arise. The arrangement most frequently found is that consisting of an inner cylinder of xylem inclosing a strand of phloem (fig. 5). From this cylinder strands of xylem radiate to

the protoxylem points. The condition is very similar to the characteristic stele described for *L. Billardieri*. The inner cylinder does not remain intact through any great length of stem, but is frequently broken up and gives rise to a parallel-banded arrangement or reverts to the radial arrangement.

Summary

1. The 2 points of interest in the study of the anatomy of *Lycopodium reflexum* are the presence of typical cortical roots and the various "types" of stele in the stem.

2. The development and differentiation of the tissues in the steles of the cortical roots parallel those in the stele of the stem.

3. There are 3 arrangements of the xylem: radial, parallel-banded, and a radial arrangement so modified as to consist of an inner cylinder of xylem inclosing a small strand of phloem. The last is the most frequently found.

4. The study confirms my former suggestions that all arrangements of xylem may occur in the same stem in species of *Lycopodium*.

The Pennsylvania State College
State College, Pa.

CURRENT LITERATURE

NOTES FOR STUDENTS

Permeability.—Further evidence against CZAPEK's theory of protoplasmic permeability is offered by Miss WILLIAMS,[1] who finds that immersion of tissues of *Saxifraga umbrosa* in certain electrolytic solutions, aluminum, potassium, and barium chlorides, potassium and barium nitrates, produces abnormal permeability to 0.2 per cent ferric chloride. Penetration was evidenced by reaction with tannin. The time of immersion required to bring about the change varied somewhat with the electrolyte, and greatly with the concentration employed. In all the electrolytes used, except barium chloride, plotting logs of time against logs of concentration in gram-mols per liter gave approximately straight lines. The abnormal permeability to iron chloride was induced without rendering the protoplasm permeable to colored cell sap in certain cells, and at surface tensions far from that considered critical by CZAPEK.—C. A. SHULL.

Colorimeter and indicator method.—DUGGAR[2] and DODGE have devised a method of obviating the interference of colored biological fluids with the indicator method of P_H determination. This is accomplished by placing equal layers of the colored test fluid on each side of a colorimeter; that on the left side receives the indicator, that on the right serves simply as a color blank. Equal layers of standard solution are also placed on each side; that on the right receives the indicator, that on the left serves as a blank.—J. J. WILLAMAN.

Flora of the Congo.—WILDEMAN[3] has resumed the publication of his studies of the Congo flora, which is prolific in new species. In the 5 fascicles just distributed, 334 new species are described, representing 39 families. The most largely represented families are Orchidaceae with 58 new species (27 of which belong to *Angraecum*) and Gramineae with 33 new species. Only 2 new genera are described, one in Leguminosae (*Pynaertiodendron*), and the other in Cucurbitaceae (*Bambekea*).—J. M. C.

[1] WHLLIAMS, MAUD, The influence of immersion in certain electrolytic solutions upon permeability of plant cells. Ann. Botany **32**:591–599. 1918.

[2] DUGGAR, B. M., and DODGE, C. W., The use of the colorimeter in the indicator method of H ion determination with biological fluids. Ann. Mo. Bot. Gard. **6**:61–70. 1919.

[3] WILDEMAN, E. DE, Florae Congolensis. Bull. Jard. Botanique Bruxelles **4**:361–429. 1914; **5**:1–108. 1915; **5**:109–268. 1916; **6**:1–129. *pls. 35.* 1919.